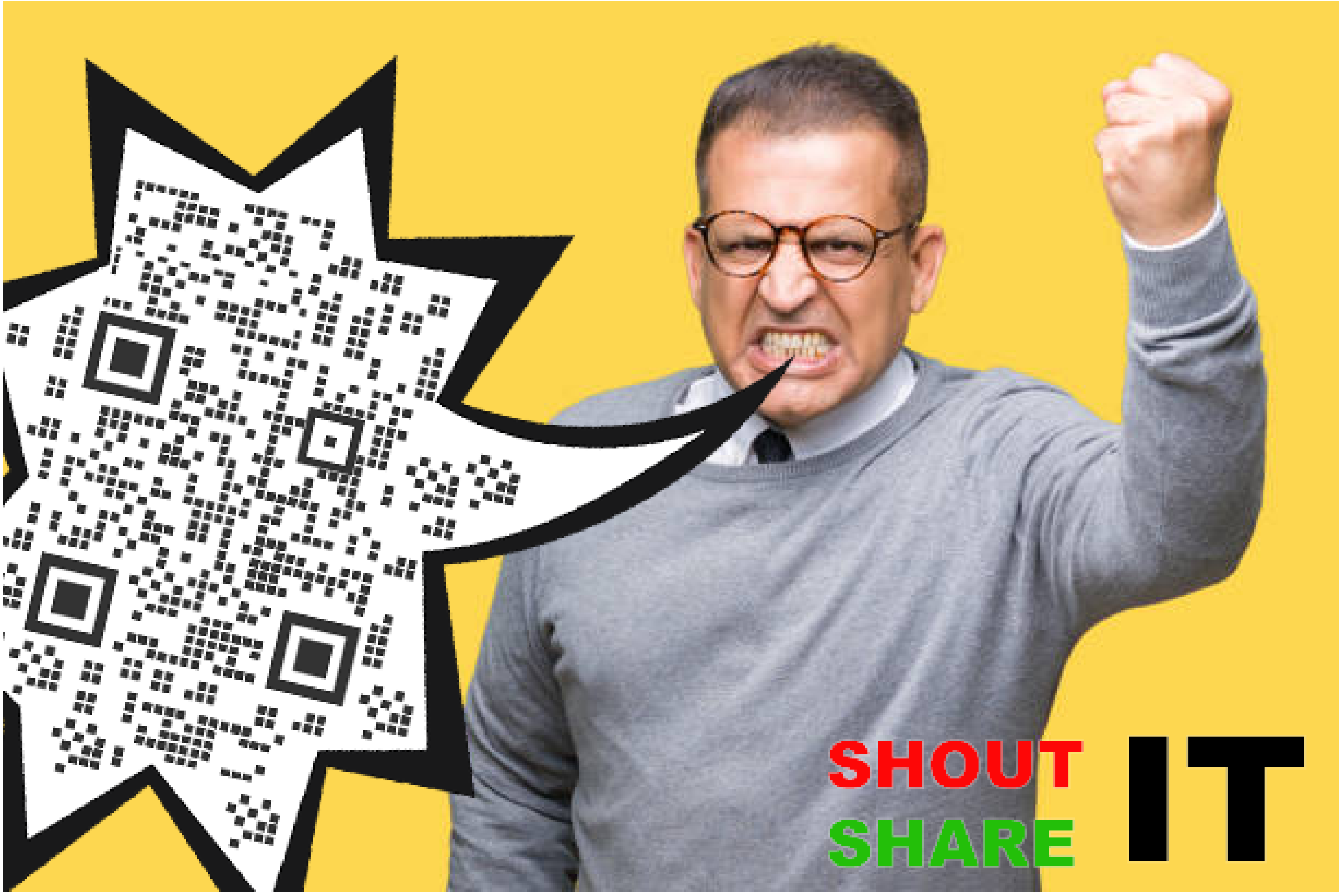
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THE *OEDURA TRYONI* COMPLEX: EAST AUSTRALIAN ROCK-DWELLING GECKOS. (REPTILIA : GEKKONIDAE)

H. ROBERT BUSTARD

BULLETIN OF
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THE *OEDURA TRYONI* COMPLEX: EAST AUSTRALIAN ROCK-DWELLING GECKOS. (REPTILIA : GEKKONIDAE)

BY

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Pp. 1–14; 3 *Plates*; 2 *Text-figures*

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TRUSTEES OF
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THE *OEDURA TRYONI* COMPLEX: EAST AUSTRALIAN ROCK-DWELLING GECKOS. (REPTILIA : GEKKONIDAE)

By H. ROBERT BUSTARD

SYNOPSIS

Following an historical review of the genus *Oedura* Gray the specific distinctness of *O. tryoni* De Vis from *O. marmorata* Gray is confirmed. *O. tryoni* as previously recognized is shown to be a complex comprising two distinct species one of which is described as new. The two species are geographically isolated, the nearest populations being five hundred miles apart. Since the original type material of *O. tryoni* has been lost a neotype is proposed for *O. tryoni* in the interests of stability. Aspects of the ecology are discussed.

INTRODUCTION

THE genus *Oedura* is morphologically divided into two groups. One group comprises *Oedura robusta* Boulenger and the two subspecies of *O. lesueurii* (Dum. & Bibr.) and is characterized by minute granular dorsal scales. The other possesses moderately large, flat, juxtaposed dorsal scales arranged in regular rows ; it includes *O. marmorata* Gray which, as currently defined, contains two distinct species, and *O. monilis* De Vis and *O. tryoni* De Vis. The geckos previously referred to as *O. tryoni* form a discrete group of predominantly rock-dwelling *Oedura* which can be divided into two forms on the basis of morphology, size, coloration and geographic distribution. *O. tryoni* as recognized by Cogger (1957) is herein split into two species and the variation within them is discussed.

Collections of *Oedura* are expanding rapidly, as is the increase of ecological knowledge of the genus, and it is now possible to examine the status of the forms grouped together as *Oedura tryoni*. Before describing the *Oedura tryoni* complex it is necessary to review the status of certain other members of the genus, since absence of clear-cut morphological differences has caused considerable confusion.

Since 1944 when Loveridge placed the African species in a separate genus (*Afroedura*), a decision which has recently been confirmed by osteological studies by Cogger (1964), the genus *Oedura* has been restricted to Australia and consists of *O. marmorata* Gray, 1842 ; *O. tryoni* De Vis, 1884 ; *O. monilis* De Vis, 1887 ; *O. robusta* Boulenger, 1885 ; *O. lesueurii lesueurii* (Dum. & Bibr., 1836) and *O. lesueurii rhombifer* Gray, 1845.

MATERIALS AND METHODS

At sexual maturity in *Oedura* preanal pores develop in male specimens and are accompanied by a conspicious bulge at the base of the tail. Since both of these secondary sexual characters are always lacking in females the sexes can be readily separated. It is not possible to sex juveniles.

Specimens possessing male characters are considered mature although growth continues for at least one year after attainment of sexual maturity. Adult size for a species is based on the range of size of specimens definitely identifiable as males. Specimens of about mean male size or above not showing male characters are considered as mature females. The size at sexual maturity in females is, therefore, arbitrary except when a field study is in progress, then it is defined as size at first breeding.

Throughout the paper the following abbreviations are used :

BMNH.	British Museum (Natural History)
AM.	Australian Museum, Sydney
QM.	Queensland Museum
NMV.	National Museum of Victoria

CHARACTERS OF THE GENUS *OEDURA* GRAY

(Modified after Boulenger, 1885)

Limbs pentadactyl ; digits free, all clawed, dilated at the base with raised distal joint bearing a discoid dilation which has two large plates inferiorly, separated by a long groove into which the claw is retractile. Proximal to the distal plates are two to six paired and one to six undivided plates. Upper surface covered with homogenous, juxtaposed scales ; abdominal scales juxtaposed or slightly imbricate. Pupil vertical. Body depressed. Femoral and preanal pores in the male.

HISTORICAL REVIEW OF *OEDURA TRYONI*

Gray (1842) proposed the genus *Oedura* and described *Oedura marmorata*. In 1884 De Vis described *O. tryoni*.

Oedura ocellata Boulenger, 1885 was later (1887) synonymized with *O. tryoni* by Boulenger when he received the 1884 description by De Vis based on specimens from Stanthorpe, south-east Queensland. However, examination of the six syntypes of *ocellata* in the British Museum collection has shown that five are conspecific with *O. monilis* and only one with *O. tryoni*. A lectotype will be selected from the five specimens conspecific with *monilis* and the full implications of this will be explained in a later paper.

Phyllodactylus (= *Oedura*) *castelnaui* Thominot (1889) was synonymized with *O. tryoni* by Zietz (1920). The author has examined the three syntypes of *Oedura castelnaui* and has found Zietz's action to be incorrect. *Oedura castelnaui* belongs to the *O. marmorata* complex and is being reinstated as a full species (Bustard, in prepn.).

Loveridge (1934) synonymized *O. tryoni* with *O. marmorata*. Loveridge was influenced by a specimen of *O. marmorata* from Port Darwin mentioned by Longman (1915) which had the infralabials separated by an azygous scale behind the mental, a character which Boulenger believed to be distinctive of *tryoni*.

Cogger (1957) drew attention to a differentiated population of *O. tryoni* in North Queensland and showed that it differed in interorbital and mid-body scale row counts from the southern population of the same species. He considered that they were possibly subspecifically distinct but took no action due to the lack of material at his disposal.

THE STATUS OF *OEDURA TRYONI* DE VIS

The species which possess moderately large, flat, juxtaposed, dorsal scales arranged in regular rows are similar in external morphology and differ most obviously in size, pattern of markings and coloration. The confusion concerning the validity of *O. tryoni* which led Loveridge (1934) to synonymize it with *O. marmorata* was caused in part by the inadequate material available for study. However, the main cause was the partly inaccurate description of *Oedura marmorata* given by Boulenger (1885) and based on thirteen specimens. He wrote, " mental triangular, shorter than the adjacent labials, which are in contact behind it ". This feature is certainly not characteristic of *marmorata*. Fifty-three specimens definitely identifiable as *marmorata* were examined and in fifty of these the adjacent labials did not meet behind the mental. In the remaining three specimens (A 4891 and A 4893 (both from Port Essington, N.T.) and R 12366 (one of two specimens from Yirrkala, via Darwin, N.T.), Australian Museum collection, Sydney) the adjacent labials do meet as figured by Boulenger (1885, pl. IX, 2). Boulenger also wrote, " Tail thick, short, much depressed, oval, the end tapering to a point ; its width is contained twice or twice and a half in its length, and equals at least the width of the body ". While this statement is applicable to regrown tails from certain localities, e.g. the Northern Territory, it is untrue for original tails. In this and other genera where the tail is used as a food store, its condition is entirely dependent on the nutritional state of the animal. For this reason gross tail morphology is an unreliable taxonomic character.

The result of Boulenger's error has been to throw doubt on the specific status of *tryoni* rather than to instigate a redescription of *marmorata*.

Cogger (1957) has shown that *tryoni* is a valid species, on the basis of ecological information and meristic characters. A glance at living material is sufficient to separate *marmorata* and *tryoni* on the basis of colour and markings and this also applies to most preserved material. Full details of coloration and its geographic variation are given by Cogger (1957).

Oedura tryoni is restricted to eastern Australia (parts of N.S.W. and Queensland) whereas *O. marmorata* occurs in all States on the mainland of Australia, except Victoria.

O. tryoni and *O. marmorata* can usually be readily separated morphologically by the postanal tubercles. In the case of *marmorata* there are one to four large tubercles (mostly 2–4) whereas in *tryoni* there is a single postanal tubercle. Fifty specimens definitely identifiable as *marmorata* were examined and in only one was there a single postanal tubercle. Twenty-six specimens possessed two, fifteen had three, and seven had four postanal tubercles. Fifty specimens of *tryoni* were examined and in every case there was a single postanal tubercle.

O. tryoni is therefore accepted as a distinct species. As has been indicated above there are no valid synonyms.

All the syntypes of *O. tryoni* held in the Queensland Museum have been lost. No cataloguing of material was carried out prior to 1911, and it has proved impossible to identify these specimens in spite of a thorough personal examination of all the gekkonid material held at the museum. Since *O. tryoni* has not found universal acceptance and furthermore since the *tryoni* complex is being divided into two species, it seems desirable that a neotype should be designated in the interests of stability.

The author has visited the type locality of *O. tryoni* (Stanthorpe, S.E. Queensland) and made a collection of this species on Mount Marlay, elevation 2,850 ft., a rocky hillside within the town. From this series of topotypic material a specimen consistent with De Vis' original description of *O. tryoni* is selected as neotype.

Oedura tryoni De Vis

(Plates 1, 2)

NEOTYPE. AM. R 21601, Mount Marlay, Stanthorpe, S.E. Queensland (the original type locality). Collected under rock (pl. 1) by the author and Dr. P. Maderson, September, 1964. Adult female.

DESCRIPTION OF NEOTYPE. Head large, greatly depressed, oval, eye large, snout moderately long, ear opening oblique. Body much depressed. Limbs moderate. Digits strongly dilated, less broad than the apical dilation which is moderate, rounded, as broad as long. Four pairs of broad infradigital plates under the third and fourth toes of hind feet with indication of division of the fifth plate on the third toe, followed by three to four undivided lamellae. Head covered with hexagonal or rounded, moderately sized, flattened scales, interorbitals number twenty-one, rostral four-sided, about twice as broad as high, with median cleft above ; nostril pierced between the rostral, first labial, and four nasals. The anterior nasal greatly elongated transversely, its depth contained at least twice in its breadth, in contact with its fellow on the opposite side ; eleven upper and nine lower labials, mental triangular. First infralabials deep, separated by a moderate octagonal scale below the mental. Back covered with juxtaposed flat round scales, considerably larger than those on the head and arranged in a regular transverse series, becoming markedly smaller on the flanks ; abdominal scales juxtaposed, flat, rounded, larger than the dorsal scales. Mid-body scale row count about one hundred and eight. Tail regenerated, moderate length, depressed, thick, the end tapering to a point ; the regenerated portion is covered with uniform square scales arranged like the bricks of a wall. Postanal tubercle single.

Dorsal coloration (in spirits) pale grey with interspersed scales of a donkey brown colour. Pale grey ocellate markings edged with donkey brown occur on the head, body and limbs. On the head they are conspicuous on the post-orbital to occipital region. On the body these form transverse bands of ocelli (pl. 1). In life the darker colour is honey brown ; lower surface dirty white, each scale possesses up to a dozen or more minute donkey brown spots. Dimensions : Absolute dimensions in mm. are followed by percentage of snout-vent length in brackets; snout-vent 88; tail (regrown) 58 (66); head 17 (19); snout 9 (10); orbit 4·5 (5); eye to ear 8 (9); width of head 18 (20); axilla to groin 40 (45); left fore limb length 27 (31); left fourth finger 5·5 (6); left hind limb length 31·5 (36); left fourth toe 6 (7).

DIAGNOSIS OF *O. TRYONI*. A species of *Oedura* with flat, round, juxtaposed dorsal scales about as large as the ventrals, characterized by numerous irregularly placed spots smaller than the orbit on the dorsal surfaces. The dorsal area of the head possesses a pattern of pale markings on a darker ground colour.

Referred Material in Australian State Museums and the British Museum (Natural History)

AUSTRALIA (no precise locality): (BMNH. 54.11.1.1: syntype of *O. ocellata*). NEW SOUTH WALES: Moonbi Range (AM. R 17676–17681), 13 miles N. of Bendemeer (between Tamworth and Armidale) (BMNH. 1964.1503–1508; AM. R 21608–21612), Inverell (AM. R 1947 and R 20952; BMNH. 96.7.1.5), Port Macquarie (AM. R 15092), 16 miles S. of Tenterfield on the road from Glen Innes (BMNH. 1964.1502), Tenterfield (AM. R 13118), Bundarra (AM. R 15649), Moree (AM. R 1815). QUEENSLAND: Dalby (AM. R 17772–17774), Chinchilla (AM. R 2801–2805; QM. J 12591–12598 and 12600), Brisbane (AM. R 18310), Eidsvold, Upper Burnett River (AM. R 5404–5408, R 5307–5309, R 5832, R 6210), Maryborough (AM. R 20991 and R 20994), Cooroomon, near Rockhampton (BMNH. 1926.2.25.21). Emuford (AM. R 15641), Fletcher (NMV. D 131), 3 miles west of Amiens (NMV. D 9314–9319, 9321–9323, 9325–9347, AM. R 21605–21606), near Pozieres (AM. R 21607), Boonah (QM. J 6418), Bell, Darling Downs (QM. J 2294), Woodford, N.C. Line (QM. J 3870), Warwick (QM. J 1354), 5 miles N. of Warwick (BMNH. 1964.1509–1510, Gympie (QM. J 12390, J 12391–12395), Alum Rock Station, via Amiens (QM. J 11975; BMNH. 1964.1511–1512), near Tara (BMNH. 1964.1501; AM. R 21613), Mount Marlay, Stanthorpe, (AM. R 21602–21604; BMNH. 1964.1496–1500).

VARIATION. (1) Subdigital lamellae. On the fourth toe of the hind foot of *tryoni* there are 4–6 divided subdigital lamellae (75% possess 4), followed by 1–4 (usually 3) undivided ones. That is, omitting the distal plates, *tryoni* possesses 6–8 enlarged subdigital lamellae, in over 70% of those examined 7 or 8.

(2) There is some variation in the number of labials; upper 10–12, lower 9–12.

(3) The variation in interorbital scale and mid-body scale row counts is illustrated in text-fig. 1. A detailed examination of the geographical variation in interorbital and mid-body scale row counts was made to see if these variations were clinal. No correlation was found to exist between latitude and scale counts.

(4) The variation in the pattern of markings is illustrated in pl. 2. Almost all specimens are characterized by well defined ocelli on the upper surface. Exceptional specimens (for example BMNH. 1964.1501, pl. 2 collected at Tara, South Queensland) have these replaced by numerous very small spots. There is little variation in coloration the ground colour being brown or grey-brown and the ocelli cream or creamy-yellow. The main variation occurs in the arrangement of the ocelli which

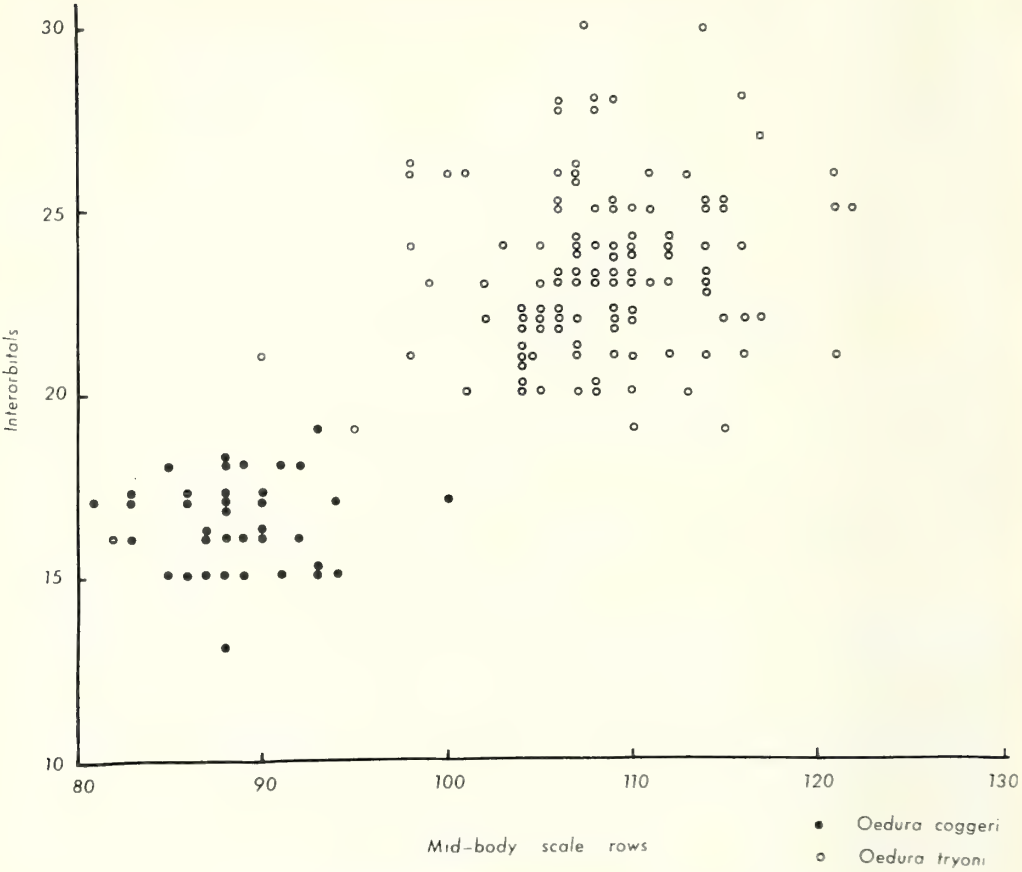

FIG. 1. Counts of mid-body and interorbital scales in *O. tryoni* and *O. coggeri*.

are usually placed transversely. Complete fusion forming continuous transverse bands never takes place, the individual ocelli invariably remain distinct, see below. The colour pattern of the northern populations of *tryoni* does not resemble *coggeri* more closely than that of the southern populations. Although populations of *tryoni* can be separated by slight differences of colour and pattern these do not form a north-south cline.

(5) Dimensions. The dimensions of 6 adult topotypic *tryoni* (BMNH. 1964. 1496–1499 and AM. R 21602–21603) are given below. No sexual dimorphism was found in any of the measurements taken. Averages are bracketed : Snout-vent 71–84 (78) mm., tail (where original) 77 (one only) ; head 21–23 (22) ; snout 9–10 (9) ; orbit 5 ; eye to ear 8–9 (8·5) ; width of head 20–21 (21) ; axilla to groin 41–44 (43) ; left fore limb 26–31 (29) ; left fourth finger 6–7 (6) ; left first limb 36–40 (38) ; left fourth toe 7–8 (7). The snout-vent length of 60 adult *tryoni* is 52–98 (77) mm. The smallest and largest males have a snout-vent length of 52 and

88 mm. respectively. There is no evidence to suggest a cline of decreasing size with decrease in latitude, the size range being similar in the north and south of the geographic range of the species.

The form previously considered as the northern population of *O. tryoni* was found to be markedly smaller and of a very variable colour pattern. There is considerable overlap in body colour pattern between the two species, but constant pattern differences occur on the head (see diagnosis). The northern population possess a lower average subdigital lamellae count, and much larger and thus fewer interorbital and body scales than the southern population of *O. tryoni*. Text-fig. 1 shows that on the basis of scale number (i.e. number of interorbitals and number of scales in a mid-body scale row around the circumference of the body) the two populations can be completely separated. In general the two forms can be separated on either scalation character. However, there is a region, shown in text-fig. 1, where there is overlap in either character used alone but if the two characters are used together a line of difference separating all individuals of the two species can be clearly defined.

The degree of morphological differentiation between *tryoni* and *coggeri* in a genus where morphological differences even between sympatric species are slight, the demonstrated fact that the differences in scale counts, pattern of markings and size are not clinal in nature and the marked geographical isolation of the two species (both have discrete geographic ranges, see text-fig. 2) has led the author unhesitatingly to describe the northern population as a new species.

Oedura coggeri sp. n.

(Pls. 1, 3)

HOLOTYPE. AM. R 17791—Lappa Junction, North Queensland, Australia, collected under rock by Mr. W. Hosmer, 24th January, 1954. Adult female.

PARATYPES. All localities mentioned are in North Queensland: Lappa Junction (AM. R 17783–17790, R 17793–17803), Petford (AM. R 17629–17631 and R 17771), Herberton (AM. R 16679), Emuford (AM. R 15641), Irvinebank (AM. R 15644), Hartley's Creek, nr. Cairns (AM. R 17767–17770), Mt. Garnet (BMNH. 1964.1494; QM. J 9290), 81 miles N.W. of Cairns on road to Laura via Mt. Carbine (BMNH. 1964.1495), Stannary Hills (QM. J 1293–5), Ravenshoe (BMNH. 1923.10.13.1–2).

DESCRIPTION OF HOLOTYPE. Head large, greatly depressed, oval, eye large, snout moderately long, ear opening oblique. Body much depressed. Limbs moderate. Digits strongly dilated, almost as broad as the apical expansion, which is moderate, rounded, as broad as long. Four pairs of broad infradigital plates under the third and fourth toes of hind feet, followed by two or three undivided ones. Head covered with uniform hexagonal or rounded, large flat scales, interorbitals number fifteen, rostral four-sided, at least twice as broad as high, with median cleft above. Nostril pierced between rostral, first labial, and four nasals. The two upper nasals large, the transverse length of the anterior nasal about equal to its depth, the supranasal in contact with its fellow on the opposite side. Ten upper and ten lower labials, mental triangular. First infralabial deep, separated by a large octagonal scale below the mental. Back covered with juxtaposed flat round scales, of a similar size to those on the head, arranged in a regular transverse series, not becoming markedly smaller on the flanks. Abdominal scales juxtaposed, flat, rounded, of a similar size or slightly larger than the dorsal scales. Mid-body scale row count about eighty-eight. Tail regenerated, moderate length, depressed, not noticeably thick, the end tapering to a point ; the regenerated portion is covered with equal square scales arranged like the bricks of a wall. Postanal tubercle single. Dorsal coloration fawn with dark brown reticulate markings continued on to the limbs and tail. A dark line along the upper border of the snout immediately above the supralabials, commencing at the rostral, passing through the eye and forming a " V-shaped " marking on the nape of the neck. Postorbital to occipital region of head unmarked (pl. 1). Lower surfaces cream.

Dimensions. Absolute dimensions in mm. are followed by percentage of snout-vent length in brackets : snout-vent 65 ; tail (regrown) 34 (52) ; head 16·5 (25) ; snout 7 (11) ; orbit 4 (6) ; eye to ear 6·5 (10) ; width of head 13·5 (21) ; axilla to groin 30 (46) ; left fore limb length 20 (31) ; left fourth finger 3·5 (5) ; left hind limb length 26 (40) ; left fourth toe 5 (8). The smallest and largest males of *coggeri* have a snout-vent length of 44 and 68 mm. respectively.

Variation among the Paratypes. The following characters are subject to variations :

(1) Subdigital lamellae. On the fourth toe of the hind foot of *coggeri* there are 3–4 divided subdigital lamellae (both occur in equal proportions), followed by 1–3 (usually 2) undivided ones. That is, omitting the distal plates, *coggeri* possesses 5–6 enlarged subdigital lamellae. The overlap in number with *tryoni*, however, prevents the lamellar arrangement being used as a diagnostic feature.

(2) Occasionally (in AM. R 17784–17785 and 17802) there is only one small nasal instead of two. The presence of two large nasals is constant.

(3) There is considerable variation in the labials ; upper 8–12, lower 8–11.

(4) The variation in interorbital scale and mid-body scale row counts is illustrated in text-fig. 1. As with *O. tryoni* a test was made for a north-south clinal variation in scale counts. No evidence for this was found.

(5) There is considerable variation in the pattern of markings. Juveniles are brown with circular or transverse cream markings. In adults the ground colour is cream to brown. Some specimens possess dark brown reticulate markings. In many specimens these enclose oblong or circular patches of cream colour. In others there are definite cream spots outlined in dark brown on the dorsal surface. The ventral surface is white. This pattern variation is not clinal, even within a single series—14 specimens from Lappa Junction—the range of colour pattern is very great, the three basic types outlined above being present (pl. 3).

(6) Dimensions. No sexual dimorphism was found in any of the measurements taken. Separate figures are given where differences occur between adults and juveniles. Figures other than snout-vent length are given as percentage of snout-

vent, averages are bracketed: snout-vent: adults 50–70 (61) mm., juveniles 33–43 (37) mm.; tail (where original) 53–78 (66); head: adults 24–28 (26), juveniles 28–30 (29); snout: adults 10–12 (11); juveniles 11–13; orbit: adults 6–7 (6), juveniles 7–8 (7); eye to ear 7–11 (10); width of head: adults 18–23 (21), juveniles 21–24 (22); axilla to groin 34–46 (41); left fore limb 24–34 (30); left fourth finger: adults 5–7 (6), juveniles 6–7 (7); left hind limb 34–44 (40); left fourth toe: 6–9 (7).

DIAGNOSIS OF *O. COGGERI.* A species of *Oedura* with flat, round, juxtaposed, dorsal scales about as large as the ventrals, characterized by numerous irregularly placed spots much smaller than the orbit. The spots frequently coalesce to form transverse cross bands (pl. 3).

The spotted specimens of *coggeri* can be separated from *tryoni* by the possession of a pale unspotted area in the postorbital to occipital region of the head. This area is bounded by a line running along the side of the head, passing through the eye, and joining with its neighbour at the nape of the neck.

DISTRIBUTION AND HABITAT

The distribution of *Oedura coggeri* and *O. tryoni* is shown in text-fig. 2. Neither species penetrates far inland and both are probably restricted to Eastern Australia.

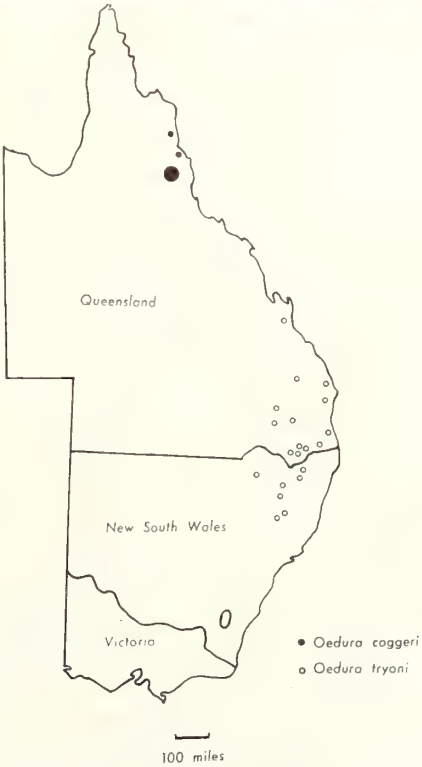

FIG. 2. Distribution of *O. tryoni* and *O. coggeri*.

The two species are separated by a gap of over five hundred miles in which to date no specimens of either species have been collected. As with *O. marmorata* suitable habitat occurs in this region and this has been searched by the author so far without success.

The ecology of *Oedura tryoni* has been examined recently (Cogger, 1957) and *Oedura coggeri* appears to occupy a similar niche. Both species seem generally to inhabit rock crevices but some individuals live on trees. Of the two specimens of *coggeri* collected in North Queensland by the author (p. 9) one was under the bark of a dead iron bark tree (*Eucalyptus* spp.) at a height of four feet from the ground and the other under a slab of a large granite boulder forming part of a low granite outcrop in *Eucalyptus* savannah-woodland. Prolonged searching failed to locate further specimens at either locality.

DISCUSSION

O. coggeri is by far the smallest species of the group possessing flat, round, juxtaposed dorsal scales, which also includes *marmorata, monilis* and *tryoni*. The species *marmorata, monilis* and *tryoni* are most readily separated by coloration which Cogger (1957) has convincingly shown to be a reliable character. *O. marmorata* possesses about five or six light-coloured cross bands. In many geographical areas these bands break up in adults and the resultant light patches are irregular in shape and size. *O. monilis, tryoni* and some specimens of *coggeri* are the only species of *Oedura* characterized by spots. *O. tryoni* and some *coggeri* possess numerous, irregularly placed, small, light-coloured spots. The distribution and size of these spots is diagnostic as pointed out by Cogger. In *tryoni* and *coggeri* the spots are numerous and much smaller than the orbit whereas in *monilis* they are much fewer in number (typically only five or six pairs which may show various degrees of fusion), and are at least as large as the orbit. *O. monilis* possesses a conspicuous, pale-coloured " V-shaped " marking or nuchal band on the nape of the neck, formed by the fusion of two ocelli. This characteristic band is usually absent in *tryoni* and *coggeri,* and is to be distinguished from the dark lines along the upper border of the snout which may join to form a "V" in some specimens of *coggeri* (e.g. the holotype, pl. 1). Another useful character, Cogger (pers. comm.), is the presence in *monilis* of a light area on the side of the head with its upper edge extending from the angle of the mouth to the ear and thence to about the insertion of the fore limb. This is typically absent in *tryoni* and *coggeri*.

Morphological differences in relative scale size are summarized in text-fig. 1.

The relationship of *O. coggeri* to other members of the genus can be considered only tentatively at present. The author considers that *coggeri* is probably the northern representative of *tryoni*. *O. tryoni* may at one time have had a continuous distribution from New South Wales through South-East and East-Central Queensland to the Cape York Peninsula. Geographic isolation of the two populations at a later time led to the observed speciation. Although *tryoni* has been considered strictly rock dwelling (Cogger, 1957), in several localities the author has found specimens on trees (*Eucalyptus* spp. and *Acacia harpophyla*) and it is possible that formerly this habitat was much more extensively used. Competition may have prevented the continued exploitation of this habitat and present day *tryoni* and *coggeri* populations mainly occur in rock crevices. At Mount Garnet the northern population of *O. marmorata* and *O. lesueurii rhombifer* were common below the bark of dead trees (*Eucalyptus* spp.) in the area where the specimen of *O. coggeri* was collected. The three forms are also known to be sympatric in a area between Atherton and Mt. Garnet.

The distribution of *tryoni* and *coggeri* is closely paralleled by the distribution of *Oedura marmorata* in Eastern Australia where there is a geographical gap of some 500 miles between northern and southern populations. The northern population of *O. marmorata* has twice received specific recognition (as *castelnaui* and *mayeri* Garman (1901)) and is to be separated from *O. marmorata* occurring elsewhere in Australia and restored to specific status following an Australia-wide study on the *O. marmorata* complex (Bustard, in prepn.).

Oedura coggeri is named after Mr. Harold G. Cogger, Curator of Reptiles and Amphibians in the Australian Museum, Sydney, in recognition of his pioneer work in applying the results of ecological investigation to the systematics of this difficult genus.

The author's collection of twenty-two specimens has been deposited in the British Museum (Natural History) and the Australian Museum, Sydney.

SUMMARY

A detailed examination of museum material together with ecological field collecting has confirmed the specific distinctness of *Oedura tryoni* De Vis. *O. tryoni* as currently defined is shown to comprise two species. *O. coggeri* n. sp. is described from North Queensland. It is tentatively suggested that *O. coggeri* differentiated from *O. tryoni* following geographic isolation. The syntypes of *O. tryoni* have been lost and a neotype is proposed in the interests of stability.

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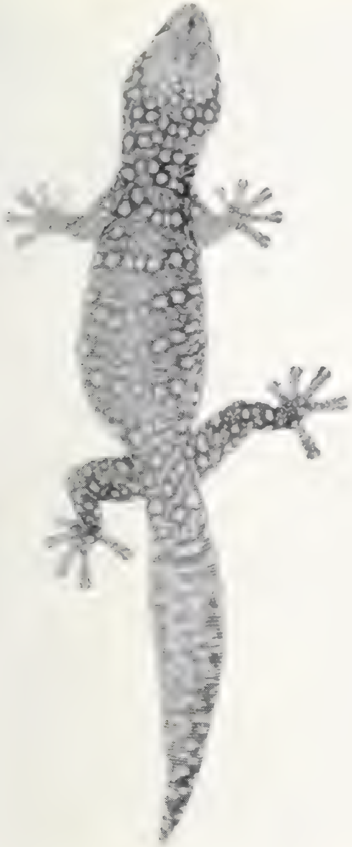
PLATE 1

UPPER ROW (left to right) : neotype of *Oedura tryoni* De Vis, holotype of *Oedura coggeri* n. sp. LOWER ROW : *O. tryoni* habitat at Mr. Marlay, Stanthorpe. The neotype was collected from under the slab at bottom centre.



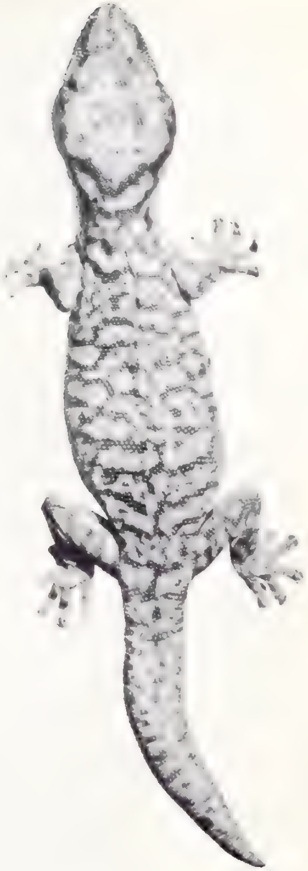


PLATE 2

Top row (left to right): *O. tryoni* juvenile from type locality (Stanthorpe), adult *Acacia* dwelling variant from Tara, S. Queensland and juvenile from 13 m. north of Bendemeer.

Middle and bottom rows: Variation among adult topotypic *O. tryoni*.

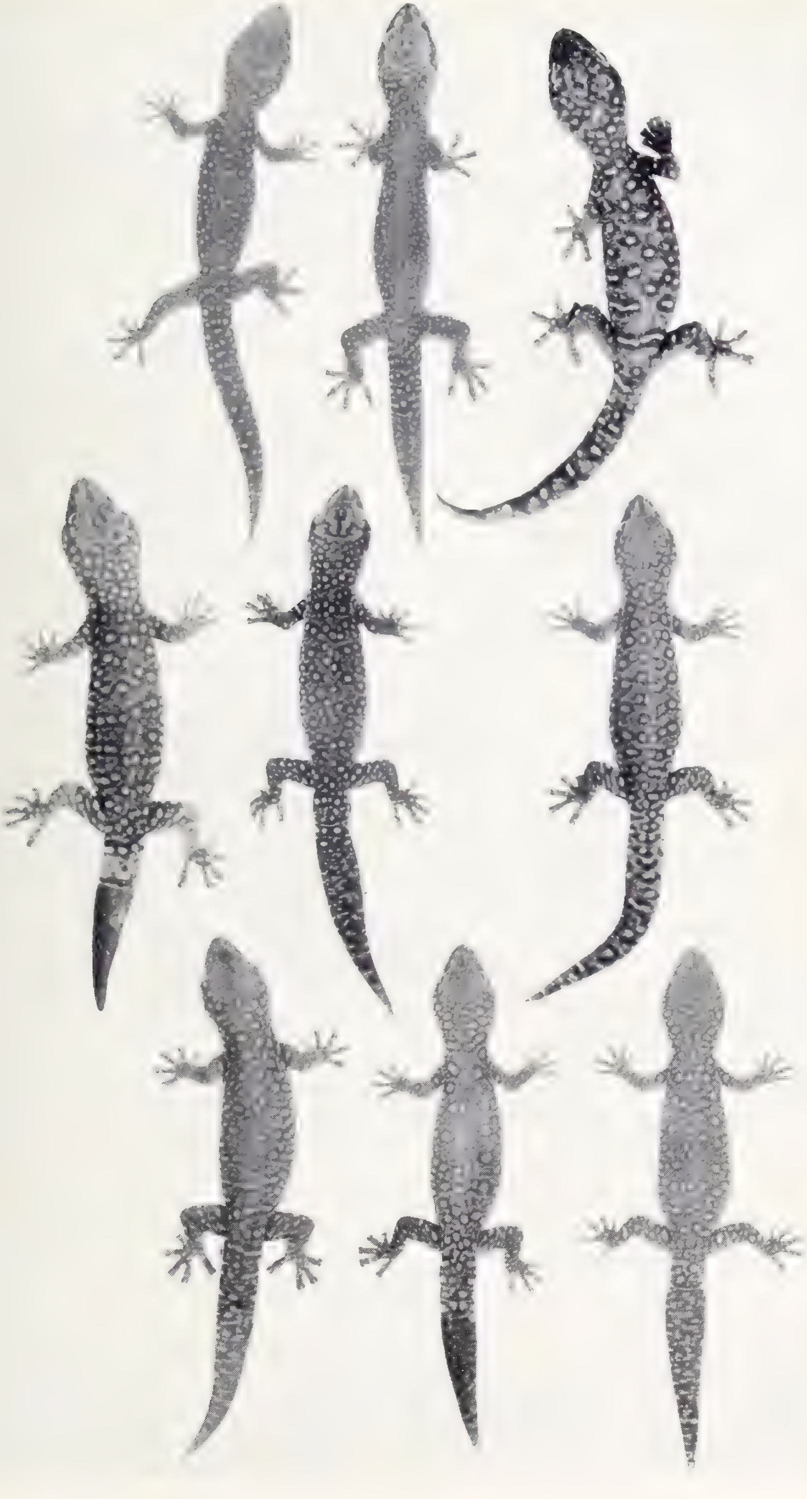
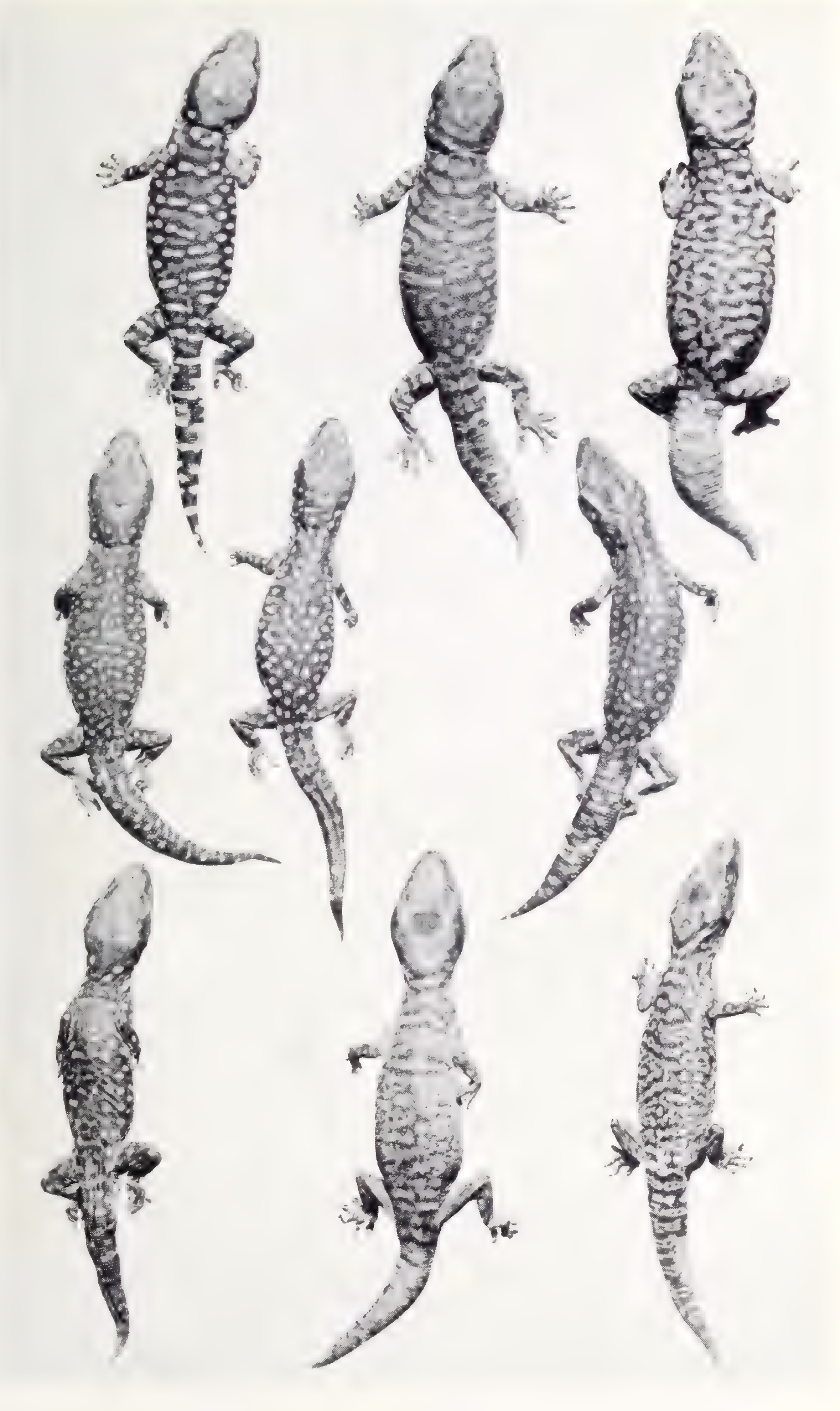


PLATE 3

Variation among *O. coggeri*. TOP ROW: Petford. MIDDLE ROW: Hartley's Creek, near Cairns. BOTTOM ROW: Lappa Junction.



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P. J. P. WHITEHEAD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 14 No. 2
LONDON: 1966

MUSEUM
TRING

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BY

P. J. P. WHITEHEAD

British Museum (Natural History)

Pp. 15–54 ; *7 Plates*

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THE ELOPOID AND CLUPEOID FISHES IN RICHARDSON'S "ICHTHOLOGY OF THE SEAS OF CHINA AND JAPAN" 1846

By P. J. P. WHITEHEAD

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ABSTRACT

The twenty-one elopoid and clupeoid fishes included by Richardson in his *Report on the Ichthyology of the Seas of China and Japan* are critically examined in the light of the specimens and the hitherto unpublished Reeves illustrations in the British Museum (Natural History). Sixteen of these species are considered valid, and the type status of certain of the specimens is established. A list is given of thirty-four elopoid and clupeoid species recorded from the Hong Kong area, and ten further species likely to occur there.

INTRODUCTION

While studying certain herring and anchovy species, it became necessary to examine those species included by Richardson in his *Report on the Ichthyology of the Seas of China and Japan*, published in 1846. Since Richardson's " Report " was based partly on specimens in the British Museum (Natural History) and partly on a collection of coloured illustrations compiled by John Reeves, also now in the British Museum (Natural History), the opportunity was taken to make a critical assessment of all twenty-one of the elopoid and clupeoid species reported by Richardson. The results have shown that a similar study of other groups would clear up many of the doubts and errors which have surrounded some of Richardson's species.

Over three hundred of the species listed by Richardson in the " Report " were represented by a Reeves illustration based on specimens from the markets at Macao and Canton. The Reeves illustrations are thus an important, sometimes decisive, factor in the identification of certain of Richardson's species. Unfortunately, the illustrations have never been published and ichthyologists have not always had the opportunity for consulting them. The twenty drawings covered by the present work are therefore reproduced here.

A full list of the herring-like fishes in the Hong Kong area has not yet been published. Since identification of the Richardson fishes has entailed an assessment of all Hong Kong–Canton records, I have compiled a tentative list of forty-four species for this area (Table 2). Richardson mentioned twenty-one species but four of these are here considered synonyms, and one cannot be identified (Table 1).

RICHARDSON'S "REPORT"

For various historical reasons, knowledge of the fishes of the seas of China and Japan lagged far behind that of European waters by the beginning of the nineteenth century. In the *Chinensia Lagerströmiana*, Linnaeus (1754) listed only 12 species of fish from China. In 1750, Pieter Osbeck, chaplain to a Swedish East Indiaman and a pupil of Linnaeus, examined fishes in the vicinity of Canton and he mentioned 9 species (Osbeck, 1757). Forster (1771), in an English translation of Osbeck's " Dagbok ", added a further 9 species given by Linnaeus in the *Systema Naturae* (or in the *Amoenitates Academicae*), to make a total of only 18 Chinese species described in the Linnaean method at that time. Boeseman (1947) has pointed to the equally sparse knowledge of Japanese fishes during the eighteenth century and in fact up until the publication of the ichthyological volumes of the *Fauna Japonica* in 1842–50.

Richardson's " Report " was one of a number of important ichthyological works which appeared at the middle of the nineteenth century. The works of Bleeker, Temminck & Schlegel, Günther, and Cuvier & Valenciennes, all dealing (in part at least) with fishes from the western Pacific, appeared at this time. The " Report " was published in the same year as that part of the *Fauna Japonica* dealing with clupeoid fishes, and it pre-dates the clupeoid volumes of Cuvier & Valenciennes (vols. 20 and 21) and also Günther (vol. 7), as well as most of Bleeker's papers. Unfortunately, due to curatorial errors and the fact that the Reeves illustrations were never published, some of Richardson's species have been ignored for so long that they are now *nomina oblita*.

Richardson based the " Report " chiefly on the coloured illustrations of John Reeves (1774–1856), supplemented by specimens from various collections. Of the latter, the fishes sent by John Reeves himself from Macao and Canton must be considered the most important since some of these were the actual models from which the drawings were made. Reeves' son, John Russell Reeves (1804–77), also resident in Macao, sent further specimens to the British Museum, although certain of the latter were " not figured in his father's drawings " according to Richardson (" Report ", p. 189). The British Museum specimens are mostly labelled J. R. Reeves, even where the " Report " implies that they were collected by the father not the son. The remainder are merely labelled " Reeves ". Richardson based 26 of his new species on specimens sent by John Reeves (or his son).

Unfortunately, the elopoid and clupeoid specimens presented by Reeves (and no doubt this is true of other groups also) were not registered, although most were listed in Günther's catalogue. The consistent omission of registration numbers on the Reeves clupeoid specimens suggests that they were presented prior to the adoption of the present registration system (in 1837). The three specimens listed here which were registered were all from the Haslar Hospital Museum. Richardson was Medical Inspector of Naval Hospitals at about this time.

A second collection of fishes studied by Richardson was that made by the Rev. George Vachell, who was Chaplain to the India Company in Macao in about 1830. The Vachell collection, of about a hundred fishes, was deposited with the Cambridge Philosophical Institution. According to Shipley (1913) the Philosophical Society Collection was transferred in 1865 to the Museum of Comparative Anatomy and

Zoology, but for several years was maintained as a separate collection. In 1866, time was spent in " overhauling these collections[1], eliminating useless or decayed specimens ". In 1866–67 Günther examined the Vachell, Darwin and Lowe collections of fishes at Cambridge, and he included a note on at least some of the species represented in the subsequent volumes of the *Catalogue of Fishes in the British Museum*, e.g. *Clupea fuegensis* and *C. arcuata*, but not the Darwin type of *C. sagax* (although it was evidently there since it was later (1917) transferred to the British Museum).

Richardson based 22 of his new species solely on Vachell specimens. Only one such type is involved in the present study, *Chatoessus maculatus*. However, this specimen appears to have been lost (see p. 37).

In addition to the Reeves and Vachell specimens, Richardson based a further 16 new species on specimens already in the British Museum (mainly presented by the Haslar Hospital, but a few from other sources).

Richardson's descriptions are often brief and one could wish for additional notes, especially when type designations are required. There is an interleaved copy of the " Report " in this museum, but it contains only a few short alterations or additions by Gray, who was then Keeper of Zoology. At about this time Gray had compiled a manuscript catalogue of the British Museum fish specimens. Unfortunately, only the " Chondropterygii " section was published (Gray, 1851), and the remainder appears to be lost. The Reeves specimens would have been listed here and this might well have resolved such puzzles as the disappearance of the type of *Clupea nymphaea* (see below, p. 24).

On Richardson's death, a bundle of his notes, drawings and some published figures were offered to the British Museum by his son. The notes were rejected, but the figures kept. However, the latter have little relevance to the present study, except perhaps for some tracings of certain of Forster's drawings of Australian fishes (from the second of Cook's voyages) (see below, *Megalops cyprinoides*, p. 44).

Compared with other ichthyological works of the time, Richardson's " Report " is a slender volume of a little over a hundred pages. However, some 665 species are listed from Chinese (or Japanese) waters, an enormous increase on any previous list. (Lacepède and Schneider knew about fifty Chinese species at the beginning of the nineteenth century.) Of these, 142 were described as new species or varieties. The " Report " would undoubtedly have been enriched by reproduction of the Reeves illustrations since 83 (or over half) of Richardson's new species were based solely on a Reeves drawing. But, although the " Report " was in many ways overshadowed by the *Fauna Japonica*, it dealt with certain tropical species not encountered in Japanese waters, and many of Richardson's species are still accepted today.

THE REEVES ILLUSTRATIONS

In the Zoological Library of the British Museum (Natural History) are certain original sets of drawings, some of which were published (e.g. the Hardwicke illustrations of Indian fishes by Gray, 1830–35). Others, such as the drawings by Forster, Parkinson and Ellis, made during Cook's voyages, have never been published. The

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[1] This statement from Shipley (1913) does not refer specifically to the fish collections, although it is likely that they too were overhauled at this time.

Reeves illustrations, of which the Zoological Library has three sets, have also remained unpublished.

Richardson (" Report ", p. 188) states that " John Reeves, Esq., who was long resident at Macao, filling an important office in the employ of the India Company, with an enlightened munificence, caused beautiful coloured drawings to be made of no fewer than 340 species of fish which are brought to the markets at Canton ". Richardson then praises the drawings " which are not surpassed in the plates of any large European work of the present day ". The praise is justified: some of the illustrations would not be out of place in a modern ichthyological paper. The paintings of clupeoid fishes, often finely dusted with silver and gold, are both aesthetically satisfying and at the same time are strongly indicative of painting from " life " rather than compilation from colour notes.

According to Richardson, Reeves had four sets of these illustrations made. Three of these sets are now in the Zoological Library of this museum. Comparing the three sets, it is not possible to judge whether one particular set contains the original drawings from which the other two were copied. The standard of the individual paintings varies somewhat within each set, and good and bad figures occur in each. Neither is there any indication that the same artist was responsible for all or the majority of figures in any one set. It seems that a number of Chinese artists were employed by Reeves over a period of several years.

Also in the Zoological Library is a bound volume containing a number of lists in Reeves' hand giving dates of completion of many of the drawings, and in some cases a few brief notes and occasionally the name of the artist (Akut, Akew and Asung are mentioned). The lists are written on East India Company notepaper, watermarked 1827 and 1828, and the dates given cover the period 1828–30. Also included are some receipts listing a number of fishes by their Chinese vernacular names (in Chinese script) and a pencilled note of the artist's name and the amount paid (e.g. 2–5 dollars for a dozen or more paintings).

The four sets of Reeves illustrations can be commented on briefly.

A. *The Reeves Set*

A bound volume of paintings with four or more fishes on each page. The pages are numbered 1–124 and each fish bears a small number, usually in red ink, sometimes in pencil. On each page these Reeves numbers run consecutively, but the order of the pages has evidently been altered, perhaps in an initial attempt to place them in systematic order. The Reeves numbers correspond with those in the lists mentioned above. The figures also bear the Chinese vernacular (presumably Cantonese) names in Chinese script, but there are no latin names (although such are used in the lists). Several illustrations are repeated (e.g. see Table 1), and in one case at least (pp. 3 and 6) almost the entire page is duplicated. At least one figure (94l) is omitted in the Richardson set.

According to one source (*Anon.*, 1904), Miss Reeves, sister of John Russell Reeves, presented her father's collection of Chinese drawings to this museum on her brother's death in 1877. In the " Report ", Richardson states that " Another copy, left by Mr. Reeves at Macao with Mr. Beale, formed the groundwork of the enumeration of

Chinese fish in Bridgman's ' Chrestomathy ' ". This might be the copy which Miss Reeves presented, since Richardson only listed two copies in the British Museum in 1846 (but see also below).

B. *The Richardson Set*

A bound volume of paintings inscribed on the fly-sheet " Sir John Richardson's set of drawings of Chinese fish by native artists (one of four) prepared under the supervision of J. Reeves (used by Richardson for his ' Report ') ".

The drawings have been cut out from their original pages and have been remounted in the systematic order adopted by Richardson in the " Report ". The pages are numbered 1–146 and several fishes are mounted on each page. Each drawing bears a small number in red ink, corresponding with the Reeves numbers in the preceding set, and the Chinese vernacular name (in Chinese script). Each drawing is also given its latin name in accordance with Richardson's text.

The figures reproduced here are taken from the Richardson set. All are reduced to the same size.

C. *The Hardwicke Set*

Four bound folio volumes amongst the Hardwicke collection of drawings contain, in addition to illustrations of Indian fishes, a set of Reeves drawings of Chinese fishes. Richardson states that these drawings were presented to General Hardwicke by Reeves and had been examined " by many English and foreign ichthyologists ", including Müller and Henle. The drawings have been cut out and remounted, and they are individually numbered in pencil (1–165, 166–313, in vol. 20a and b ; 1–174, 175–317 in vol. 21a and b). In some cases the Reeves number (in red ink) and the Chinese vernacular ideogram are present. All the Reeves drawings are named and have a page reference to Richardson's " Report ". Of the elopoid and clupeoid species, three found in the previous two sets are here missing (see Table 1). In the inter-leaved copy of the " Report " in the Zoological Library, Gray has listed about 45 Reeves drawings not represented in the Hardwicke set.

The Hardwicke drawings were presented to this museum in 1835.

D. *The " Fourth " Set*

I have been unable to trace the fourth set mentioned by Richardson nor any other reference to such a set other than those based on Richardson's statement. It is possible that the fourth set is indeed the Beale set, i.e. the Reeves set given to Beale and lent to Samuel Wells Williams, who was responsible for the Natural History section of the Chinese Chrestomathy (Bridgman, 1841). In this work, 245 fishes are listed (15 clupeoids), but their serial numbers do not tally with the numbers on the Reeves drawings. Cantonese vernacular names are given (English and Chinese script) and also the generic names ; the latter may have been derived from the drawings, but if so, then the drawings will indeed constitute the fourth set, since the Reeves set in this museum does not bear generic names.

The fourth set is not amongst the several series of paintings of Chinese fishes in the Department of Prints and Drawings nor in the Department of Oriental Printed books and Manuscripts of the British Museum ; nor is it in the Library of the India Office in London.

TA

A list of the elopoid and clupeoid species mentioned by Richardson (1846) showing pa

Species	Richardson, 1846
	(name)
ELOPIDAE	
Elops machnata (Forssk.)	*Elops machnata* Forssk. *Elops purpurescens* Rich.
MEGALOPIDAE	
Megalops cyprinoides (Brouss.)	*Megalops setipinnis* Forster *Megalops curtifilis* Rich.
CHIROCENTRIDAE	
Chirocentrus dorab (Forssk.)	*Chirocentrus dorab* Forssk.
DUSSUMIERIIDAE	
Spratelloides gracilis (Schlegel)	*Clupea gracilis* Schl.
CLUPEIDAE	
(Clupeinae)	
Sardinella aurita Val.	*Clupea nymphaea* Rich.
Sardinella fimbriata (Val.)	*Clupea isingleena* Rich.
?*Sardinella leiogaster* Val.	*Clupea caeruleo-vittata* Rich.
Sardinella or *Herklotsichthys* sp.	*Clupea flosmaris* Rich.
(Alosinae)	
Hilsa reevesii (Rich)	*Alosa reevesii* Rich. *Alosa palasah* Russell
(Pristigasterinae)	
Ilisha elongata (Ham. Buch.)	*Ilisha abnormis* Gray
(Dorosomatinae)	
Clupanodon thrissa (Linn.)	*Chatoessus triza* Linn. *Chatoessus maculatus* Gray
Konosirus punctatus (Schlegel)	*Chatoessus aquosus* Rich.
Nematalosa, ?*N. nasus* (Bloch)	*Chatoessus chrysopterus* Rich.
ENGRAULIDAE	
(Stolephorinae)	
Stolephorus commersonii Lacepède	*Engraulis commersonianus* Lac.
Thryssa mystax (Schn.)	*Thryssa mystax* Schn.
(Coiliinae)	
Coilia mystus (Linn.)	*Coilia grayii* Rich.
Coilia playfairii (Rich.)	*Coilia playfairii* (McClelland).

on numbers in the three sets of Reeves drawings now in the British Museum (Natural History).

	Illustrations—page nos.			
es ber	Reeves	Richardson	Hardwicke	Reeves specimens
	97, 99	142	30	BMNH. 1964.11.6.3
	46	142	31	—
	68	141	234	BMNH. 1964.11.6.14. Type* BMNH. 1853.1.4.20
	27, 97	141	—	—
	33	142	237	BMNH. 1964.11.6.1
	—	—	—	—
	31	136	222	BMNH. 1964.11.6.6–7 (Type lost)
	29, 95	136	219	BMNH. 1963.6.17.1 Type
	29, 95	136	223	—
	29, 95	136	—	—
	102	137	220	BMNH. 1963.8.20.2 Type BMNH. 1963.8.20.3
	96	137	221	BMNH. 1963.8.20.1
	29, 48	138 upper	—	BMNH. 1964.11.6.4. Type
	100	138 lower	240	
	53, 54	139	232	—
	91	139	233	Vachell specimen (Type lost)
	29, 95	139	230	BMNH. 1964.11.6.5. Type
	29, 95	139	231	—
	—	—	—	BMNH. 1964.11.6.8–11
	92, 97	141	236	BMNH. 1964.11.6.12
	8	140	252	BMNH. 1855.9.19.1581. Type* BMNH. 1964.11.6.2.*
	31	140	—	BMNH. 1847.5.10.5. Type*

Reeves material, *ex* Haslar collection.

RICHARDSON'S SPECIES

The twenty-one species are listed here in the order adopted by Richardson (see Table 1 for correct systematic list). Synonymies list only Hong Kong, Canton and Macao references. Type specimens are redescribed, and also certain species whose systematic position is uncertain or controversial.

1. " *Clupea isingleena* Richardson "
= ***Sardinella fimbriata*** (Valenciennes)

Clupea isingleena Richardson, 1846, *Ichth. China Japan* : 304 (China Seas).
Spratella fimbriata Valenciennes, 1847, *Hist. Nat. Poiss.* **20** : 359, pl. 600.
Clupea (*Harengula*) *kowala* : Bleeker, 1873, *Ned. Tijdschr. Dierk.* **4** : 147 (on Richardson).
Harengula nymphea : Regan, 1917, *Ann. Mag. nat. Hist.* (8) **19** : 392 ; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 599, fig. 15 ; Chu & Tsai, 1958, *Quart. J. Taiwan Mus.* **11** (1 and 2) : 115, pl. 3, fig. 1 [*non Clupea nymphaea* Richardson—see below].

TYPE. A fish, 108·5 mm. standard length, until recently unregistered and labelled " *Clupea nymphaea* TYPE China " (Pl. 1, fig. 1). Now recognized as the lost type of *C. isingleena* Richardson and registered BMNH. 1963.6.17.1 (see discussion below).

FIGURE. Reeves No. 60 shows a rather deep-bodied clupeoid (depth 2·75 in standard length) not unlike a juvenile *Hilsa kelee* (Cuvier) in shape but lacking any spots or marks along the flanks (Pl. 1, fig. 2). Dorsal rays vary between 12 and 14 in the three sets of illustrations, and anal rays from 9 to 12. However, the number of finrays shown in these drawings seems to conform more to aesthetic than to scientific standards. The figure shows a fish slightly deeper than either Richardson describes (3 times in length) or is the case with the actual specimen (3·1 times). But there is otherwise sufficient conformity between the figure, the description and the specimen for the three to relate to the same species. Since the drawing and the specimen are both 5½ inches, it is quite possible that the specimen was the actual model for the illustration used by Reeves' artist.

NOTES. There is no specimen labelled *Clupea isingleena* in the British Museum and Günther (1868, p. 429) reported the same. However, Günther (loc. cit.) recognized a specimen (of 5½ inches) as the type of *Clupea nymphaea* (Pl. 1, fig. 1), presumably because it was then labelled as such, and until now this has been accepted as the type of *C. nymphaea* (e.g. by Regan (1917*b*) in his revision). However, Günther noted that the anal ray count (21) in this specimen tallied not with the description and figure of *C. nymphaea* but with that of *C. isingleena*, as also did the size of the specimen. He then states that the " one example in the British Museum . . . belongs, on account of its oblong form, to the figure named *Cl. nymphaea* ", a statement which is certainly not true of the present specimen labelled *C. nymphaea* ; neither does it accord with Günther's own description of this specimen (" the height of body thrice and one sixth " in standard length). In the figure of *C. isingleena* the body depth is contained 2·75 times in standard length, against 3·65 times in the figure of *C. nymphaea* (3·1 in the actual specimen, " thrice in the length " according to Richardson's description of *C. isingleena*).

Since Richardson gave an adequate description of *C. isingleena*, based on a specimen (of 5½ inches) and on a drawing (also 5½ inches), and at the same time indicated the museum in which the specimen was deposited ; and since there is a British Museum specimen (of $5\frac{1}{2}$ inches) which conforms with both drawing and description in almost all respects ; then Günther's type designation must be recognized as wrong, being based on a curatorial error. The specimen in question has 8 pelvic rays. A pelvic count of 9 (described for *C. nymphaea*) is known only in one species of *Sardinella*, namely *S. aurita*, which in fact is a slender species such as is described and figured for *C. nymphaea*. In *S. aurita* too, the anal count is low (15–19 *fide* Regan, 1917*b*) and thus agrees with Richardson's *C. nymphaea* (A.15 vel 16) not with his *C. isingleena* (A.21).

One slight anomaly, however, is in Richardson's scute count of 16 + 10 for *C. isingleena* ; the specimen has 18 + 12, although one post-pelvic scute is very small. But even in *S. aurita* there are at least 13 post-pelvic scutes.

It must be accepted, therefore, that the specimen long known as the type of *Clupea nymphaea* Richardson is in fact the lost type of *C. isingleena* Richardson. However, the latter name, although pre-dating all other names for this species, has not been used as a senior synonym since Richardson's time and is therefore a *nomen oblitum*.

The type specimen was considered a species of *Harengula* by Regan (1917*b*) and subsequent workers (e.g. Fowler, 1941 ; Chu & Tsai, 1958). But it is clearly a member of *Sardinella*, having 8–10 fronto-parietal striae and upper and lower parts of the 2nd supra-maxilla similar in shape and size (see Whitehead, 1964*a*, 1964*c* for diagnosis). The vertical striae on the scales (a character used by Regan, 1917*b*) resemble those in *Harengula* or *Herklotsichthys*, appearing to be continuous across the scale, but in fact in most cases the inner ends of the striae do not meet in the centre but overlap each other (Chan, 1965, fig. 8). The anal, however, is too poorly preserved to judge whether the antepenultimate ray is significantly shorter than the final two rays (a *Sardinella* character). It is interesting to note that in neither Fowler's drawing (1941, fig. 15) nor in the description of this species by Chu & Tsai (1958) are the last two anal rays indicated as enlarged (" somewhat larger " according to Chan, 1965). Regan (1917*b*) placed emphasis on this character in his differentiation between *Sardinella* and *Harengula*, but in this species at least, it does not appear to be diagnostic.

The search for the correct name for the present species is by no means simple. Chu & Tsai (1958) list six species of *Sardinella* in the Taiwan area, as well as *Harengula nymphaea*. Of the four with 8 pelvic rays and sharply keeled scutes (i.e. excluding *S. aurita* and *S. sirm* respectively), none has a gillraker count above 63, whereas the specimen in question has 71 (or 69, Chan, 1965). A count of 69–81 and a body depth of 2·99–3·53 is given for *S. fimbriata* (Valenciennes) by Chan (loc. cit.) in his revision of the genus, and until further studies on this genus are published, this should be considered the next available junior synonym. Bertin (1944) concluded that the Valenciennes types of *Clupeonia jussieui* and *Spratella fimbriata* represented a single species (both with about 70 gillrakers). The former name has page priority over the latter, but until the identity of *Clupanodon jussieu* Lacepède is established (or the name rejected), it is best that the name *fimbriata* be retained for the present since authors have used the name *jussieu* for another species (i.e. for Bleeker's species *gibbosa* ; see also discussion in Whitehead, 1965*b*).

REDESCRIPTION OF TYPE OF *CLUPEA ISINGLEENA*

Standard length : 108·5 mm.
Total length : 140 mm. or 5½ inches (estimated since caudal tips damaged).

	mm.	%S.L.
Body depth	35·2	32·4
Head length	28·3	26·2
Snout length	5·8	5·3
Eye diam.	8·0	7·4
Upper jaw l.	11·9	11·0
Lower jaw l.	12·4	11·5
Pectoral length	damaged	—
Pelvic length	11·8	10·9
Pre-dorsal	49·1	45·3
Pre-pelvic	59·2	54·5
Pre-anal	88·5	81·5

Body strongly compressed, its depth greater than head length, snout less than eye diameter. Maxilla, reaching to eye centre but not to articulation of lower jaw, lower edge with a few minute denticulations ; exposed portion of maxilla with 4–5 longitudinal ridges ; 2nd supra-maxilla " paddle-shaped ", upper and lower parts of expanded portion similar in size and shape, length of expanded portion equal to depth ; 1st supra-maxilla slender. Pseudobranch short, its length about ¾ of eye diameter, ventral border without prominent ridge.

Dorsal surface of head with well-defined cuneiform fronto-parietal areas with 8–10 longitudinal striae. Bilobed dermal outgrowth on vertical portion of cleithrum and well-developed cleithral lobe along lower border of gill opening. Gillrakers 41 + 71 on first arch, about equal to gill filaments, neither upper nor lower series overlapping the other ; gillrakers present on posterior face of 3rd epibranchial.

No teeth in jaws but a single longitudinal series of fine teeth along tongue and numerous fine papillae on rest of tongue ; fine teeth present on pterygoids.

Dorsal origin nearer to snout than to base of caudal, but entire dorsal base equidistant between snout and caudal base ; dorsal rays iv 14, tips damaged. Pectoral with i 15 rays, tips damaged. Pelvic, with i 7 rays, its base under middle of dorsal and equidistant between pectoral base and anal origin. Anal with iii 18 rays, its origin a little nearer to caudal base than to pelvic base.

Scutes sharply keeled, 18 pre-pelvic, 12 post-pelvic. Many scales missing, exposed portions with fine perforations and longitudinal ridges leaving an almost pectinated posterior border (two scales from type figured by Chan, 1965, fig. 8).

Colour in alcohol : upper ¼ of body brown, flanks silver, fins hyaline ; no indication of dark markings.

2. " *Clupea nymphaea* Richardson "
= *Sardinella aurita* Valenciennes

Clupea nymphaea Richardson, 1846, *Ichth. China Japan* : 304.

Sardinella aurita Valenciennes, 1847, *Hist. Nat. Poiss.* **20** : 263, pl. 594 (name retained for reasons of stability—see below) ; Regan, 1917, *Ann. Mag. nat. Hist.* (8) **19** : 578 (including Günther's two specimens of *C. melanostictus* from China—see below) ; Fowler, 1931, *Hong Kong Nat.* **2** (2) : 116 (compiled, no Chinese specimens).

Clupea melanosticta : Günther, 1868, *Cat. Fish. Brit. Mus.* **7** : 430 (2 Reeves fishes and 1 juvenile *ex* China).

TYPE. No British Museum specimen. As shown under *C. isingleena*, the specimen hitherto labelled as type of *C. nymphaea* (see Günther, 1868, p. 428 ; Regan, 1917, p. 392) is in fact the type of *C. isingleena*.

FIGURE. Reeves No. β25 shows a rather slender clupeoid resembling *Sardinella sirm* or *S. clupeoides* (Pl. 1, fig. 3). It lacks any black spots or marks along the flanks such as occur in *Sardinops*. Pre-pelvic scutes are not shown, but there are 14 or 15 post-pelvic scutes (only 12 in the Hardwicke illustration). The anal base is moderate, about equal to dorsal base, and 14 rays are shown. The figure is 6¾ inches in total length (140 mm. standard length).

NOTES. The identity of this species has hitherto remained doubtful, partly due to the confusion over the type specimen. However, Richardson describes 9 pelvic rays and this immediately excludes all species of *Herklotsichthys* (*Harengula auct.*, see Whitehead, 1964*a*) and also all species of *Sardinella* except *S. aurita* Valenciennes, 1847. Of clupeoid species with rather elongate bodies, *Sardinops melanosticta* (Schlegel) can be ruled out since it has only 8 pelvic rays and the series of black spots along the flanks are obvious even in long preserved material. *Sardinella sirm* (Walbaum) is similar in form to the Reeves illustration, but it has only 8 pelvic rays and there is a series of dark spots along the flank. I have found no record of *S. sirm* from the Hong Kong area. Finally, *Clupea harengus pallasi* can be considered. But although the check list given by Liang (1951) of specimens in the Provincial Fisheries Institute in Taiwan suggests that this species is present in the area, Chu & Tsai (1958), in a review of Taiwan clupeoids, found no evidence of *C. harengus* and believed that Liang's specimens were from Japan. It is most unlikely that *C. harengus* would penetrate as far south as Macao.

By elimination, therefore, Richardson's *C. nymphaea* can only be *Sardinella aurita*. Richardson's name, however, pre-dates that of Valenciennes, and should strictly replace it ; it is not a *nomen oblitum*, having been in constant (mis)use. But the species is the most widespread and commercially important of all *Sardinella* species. In the interests of stability, therefore, it will be recommended to the International Commission that Richardson's name should be suppressed, and the name *S. aurita* Valenciennes retained.

There are two specimens of *S. aurita* in the British Museum which are labelled " *Clupea melanosticta* (TYPES) China Reeves ". They are adult fishes (160 mm. S.L.), until now unregistered, but now BMNH. 1964.11.6.67. They were listed, as Reeves specimens, by Günther (1868, p. 430) under the name *Clupea melanosticta* Schlegel. This was a misidentification, since *C. melanosticta* Schlegel is a species of *Sardinops*. Günther included a third specimen, a juvenile of 65 mm. S.L. also from China. The latter is too small and was registered too late (1851) to have been the missing Richardson type of *C. nymphaea*.

Günther (loc. cit.) placed *C. caeruleovittata* Richardson in his synonymy of *C. melanosticta* Schlegel. Richardson lists no specimens of *C. caeruleovittata*, so the present specimens cannot be types of that species. The original label on the bottle containing these two Reeves specimens is now missing (the bottle was relabelled after the war, presumably copied from the old label which had become detached). The designation of these specimens as types seems to have occurred after Günther had listed them. They are not types of *C. nymphaea* since Richardson only refers to a single " Specimen in Br. Mus." ; neither are they the types of *Clupea melanosticta* Schlegel, which are in Leiden (Boeseman, 1947). They may, perhaps, have been sent to the British Museum by Reeves' son after the " Report " was written.

3. " ***Clupea caeruleo-vittata*** Richardson "
= ***Sardinella***, probably ***S. leiogaster*** Valenciennes

Clupea caeruleo-vittata Richardson, 1846, *Ichth. China Japan :* 305 (on Reeves illustr.).

Sardinella leiogaster Valenciennes, 1847, *Hist. Nat. Poiss.* **20** : 270 ; Kner, 1865, *Reise Novara, Fische* : 327 (Hong Kong).

? *Harengula moluccensis* : Jouan, 1867, *Mém. Soc. Imp. Sci. nat., Cherbourg,* **13** (2^e ser.) (3) : 272 (Hong Kong).

Clupea (*Amblygaster*) *melanosticta :* Bleeker, 1873, *Ned. Tijdschr. Dierk.* **4** : 147 (on *C. caeruleo-vittata* Richardson).

Sardinella sirm : Fowler, 1931, *Hong Kong Nat.* **2** (2) : 119 (solely on Kner, 1865 for Hong Kong record).

SPECIMENS. No specimens mentioned by Richardson. There is none in the British Museum, except the two Reeves specimens labelled " *Clupea melanosticta* TYPES " mentioned under the previous species. Since Günther placed *C. caeruleovittata* Rich. in his synonymy of *C. melanosticta,* and since he listed two Reeves specimens, it is odd that these two fishes are not labelled as types of *C. caeruleovittata*. However, in certain cases, the most recent bottle label has been a copy, not of the original name on the old label, but of the name as later amended (by Günther, Regan, Norman, etc.). Unfortunately the original label has gone.

FIGURE. Reeves No. 59 shows an even more elongate clupeoid than the previous species, a fact commented on by Richardson (Pl. 2, fig. 1). In appearance it suggests a gravid female with distended abdomen. It resembles *Etrumeus teres* (DeKay), which occurs in Hong Kong waters (see Table 2), but the pelvics are set below the dorsal base, not well behind it. Of the remaining elongate clupeoids recorded from this area, the following can be considered : *Sardinops melanostictus, Clupea harengus, Sardinella aurita, S. sirm* and *S. leiogaster*. The first can be eliminated on grounds of coloration, there being no spots shown on the flanks in Reeves' illustration. The second can also be ruled out on geographical grounds (see discussion under *C. nymphaea*). The Reeves drawing is not accurate enough for a pelvic finray count, which would distinguish *S. aurita* (9) from *S. sirm* and *S. leiogaster* (8). But since *S. aurita* is already represented in Richardson's list (as *C. nymphaea*) under the Chinese vernacular name *Chang yaou lin* (" long-waisted scale " or " long fine waist "), it can be argued that *C. caeruleovittata*, the *Huang-tsih* (" yellow glossy ") of the " Report ", must therefore be another species. Of the two remaining elongate clupeoids, *Sardinella leiogaster* seems the more likely. It is a slightly deeper fish and lacks the row of dark blue spots along the flanks described in *S. sirm* (see Chu & Tsai, 1958).

Another possibility is *S. clupeoides* (Bleeker, 1849). Unlike Bertin (1944), Chan (1965) recognised this species as distinct from *S. leiogaster*; it has the dorsal origin nearer to snout tip than to caudal base, a feature well shown in the Reeves drawing (Pl. 2, fig. 1). However, there are no records of this species from the Hong Kong area.

Harengula moluccensis of Jouan (1867) from Hong Kong may refer to the present species, although " le ventre non caréné " is suggestive of *Etrumeus teres*. There are records of *E. teres* from Hong Kong (Whitehead, 1963*a* p. 374), and Jouan (loc. cit.) states that his fish is common (in October) (4 Hong Kong juveniles in British Museum sent by Chan). However, his pelvic count of 7 fits neither *Etrumeus* nor *Sardinella*.

Richardson's name *caeruleovittata* predates Valenciennes' name *leiogaster*. However, it has now become a *nomen oblitum*, and in view of the difficulty in making a correct identification of Richardson's species, no purpose would be served in attempting to resurrect this name.

4. " **Clupea flosmaris** Richardson "
= **?Herklotsichthys** sp. or **Sardinella** sp.

Clupea flosmaris Richardson, 1846, *Ichth. China Japan* : 305 (on Reeves' illustr.).

SPECIMENS. None mentioned by Richardson, and none in British Museum.

FIGURE. Reeves No. 64 shows a clupeoid of moderate body depth in which the scales appear to have been lost (Pl.2, fig. 2). Fowler (1931, p. 112) identified this species with *Spratelloides delicatulus* (Bennett) although admitting that the figure (6 inches) is much too large " due to an exageration of the artist's drawing ". The fish shown is too deep for *S. delicatulus*, and is most likely a juvenile *Sardinella* or *Herklotsichthys*. Richardson compared this fish with one described and figured in the " Description of Animals ", p. 201, fig. 149 (see " Report " for note on this work.) This latter description gives the following finray counts : D 13, A 19, C 14, P 10, V 9. But the anal count, and the serrated belly in the figure, rule out a round herring ; the pelvic count is virtually diagnostic of *Sardinella aurita*. However, the Reeves illustration shows an anal count of only 9, and there is no real evidence that the Reeves drawing is of the same fish as that in the " Description of Animals ".

The most that can be said of this Reeves illustration is that it is of a juvenile clupeoid, probably a species of either *Sardinella* or *Herklotsichthys*.

5. " **Clupea gracilis** Temm. et Schl. F. J. Sieb."
= **Spratelloides gracilis** (Schlegel)

Clupea gracilis Schlegel, 1846, *Faun. Japon. Poiss.*, pt. 5, pl. 108, fig. 2 (Japan) ; Richardson, 1846, *Ichth. China Japan* : 305 (?Japan).

SPECIMENS. Richardson examined a British Museum specimen (in bad condition) labelled " *Clupea gracilis* " and concluded that he could not " identify it with any of the preceding species ". I have been unable to determine which specimen this might be, but Günther (1868, p. 465) lists three Japanese specimens (registered BMNH.4.6.8134). There are Hong Kong specimens in our collection, and three Taiwan specimens have been described (Whitehead, 1963*b*, p. 343).

FIGURE. No Reeves illustration.

NOTE : I can find no published reference to this species from Hong Kong, although it is well recorded from Japan, the Philippines and also Taiwan. Fowler (1931, p. 112) reports the closely related *S. delicatulus* (Bennett) from China, but as noted earlier, this is based solely on a misidentification of Richardson's *C. flosmaris*. There are now a number of specimens of *S. gracilis* in the British Museum (BMNH. 1965.7.5.49–70) sent by W. L. Chan from Hong Kong and the species is probably not uncommon there. Whereas *S. gracilis* and *S. delicatulus* occupy roughly the same range in the Indian Ocean and along the shores of the Indo-Malayan Archipelago, in the western part of the Pacific their ranges diverge. *S. delicatulus* has the more southerly distribution, extending southwards to Tasmania, while *S. gracilis* reaches further north (to Japan). *S. delicatulus* is recorded from the Philippines (see Fowler, 1941, p. 562), but probably does not reach Hong Kong or Taiwan.

6. " ***Alosa reevesii*** Richardson "
= ***Hilsa reevesii*** (Richardson)

Alosa reevesii Richardson, 1846, *Ichth. China Japan* : 305.

Alausa reevesii : Valenciennes, 1847, *Hist. Nat. Poiss.* **20** : 437 (dry specimen from Macao) ; Jouan, 1867, *Mém. Soc. Imp. Sci. nat. Cherbourg,* **13** (2) (3) : 271 (Hong Kong).

Hilsa reevesii : Fowler, 1931, *Hong Kong Nat.* **2** (2) : 115 (China, compiled ; no Hong Kong specimens) ; Whitehead, 1964, *Bull. Brit. Mus. (nat. Hist.) Zool.* **12** (4) : 141 (revision ; type and Reeves and Hong Kong specimens).

Alosa palasah : Richardson, 1846, *Ichth. China Japan* : 306 (Reeves specimen).

Alausa palasah : Jouan, 1867, *Mém. Soc. Imp. Sci. nat. Cherbourg,* **13** (2) (3) : 271 (Hong Kong).

TYPE. A fish, 295 mm. standard length, *ex* China, presented by J. R. Reeves, until recently unregistered, but now BMNH. 1963.8.20.2. Günther (1868, p. 447) regarded this specimen as the type and mentioned a smaller Reeves specimen (140 mm. standard length, now BMNH. 1963.8.20.3). The latter, not the former, has until now been labelled as the type in our collections, but this is wrong : the smaller specimen is not mentioned by Reeves. Both are mounted skins.

FIGURE. Of the three copies of Reeves' figure *x*8 in the British Museum, that found in the Hardwicke set is the best, but all are adequate to identify the species (Pl. 2, fig. 3). Richardson states that " Mr. Reeves deposited a specimen in the British Museum which still retains the original label numbered in reference to his (Reeves') drawing ". It is not clear from this whether the drawing (17 inches) was made from this actual specimen (15 inches). There is no label now attached to the fish, but a pencilled note on the underside of the stand on which the specimen is mounted gives the Reeves number, name, locality and collector.

NOTE. The holotype is clearly *H. reevesii*, not *H. ilisha*, having the broad operculum characteristic of the former (see Whitehead, 1965*a*). In addition, there are only 15 branched anal rays (18–20 in *H. ilisha*) and the anal origin is equidistant between the caudal base and pelvic *tips* (pelvic *base* in *H. ilisha*).

Richardson records too few scales in lateral series (" Thirty of them compose a longitudinal row "), since there are at least 40 in the specimen, probably more. *Hilsa toli* (Valenciennes) also occurs in this region (see Table 2), but it has a narrow operculum (as in *H. ilisha*) and the caudal lobes exceed head length (about equal to head length in *H. ilisha* and *H. reevesii*).

REDESCRIPTION OF THE TYPE OF *CLUPEA REEVESII*

Standard length : 295 mm.

Total length : 369 mm., or 14½ inches (approx. 15 inches according to Richardson).

	mm.	%S.L.
Body depth	91·0	30·7
Head length	84·5	28·7
Snout length	21·5	7·3
Eye diam.	12·8	4·3
Upper jaw l.	35·0	11·9
Lower jaw l.	43·2	14·7
Pectoral l.	47·0	15·9
Pelvic l.	24·5	8·3
Operculum height	35·5	12·0
width	24·0	8·2
Pre-dorsal	149·4	50·5
Pre-pelvic	143·8	48·5
Pre-anal	239·0	81·0

Dorsal iii 14 (or iv 13, tips broken) ; pectoral i 15 ; anal iii 15 ; scales in lateral series about 41. In all other respects, this specimen conforms to the description given by Whitehead (1965*a*).

7. " **Alosa palasah** Russell "
= **Hilsa reevesii** (Richardson)

(See previous synonymy.)

SPECIMEN. A fish, 140 mm. standard length, *ex* China, collected and/or presented by J. Reeves. Hitherto unregistered, now BMNH. 1963.8.20.1. The bottle still bears two of the original labels, the first reading " *Clupea reevesii* China J. Reeves Esq." and the second " Reeves B51 Hard. 221 ". Richardson mentions a British Museum specimen of 7 inches ; the present specimen is 7¼ inches in total length and is undoubtedly that examined by Richardson.

FIGURE. Reeves No. β51 shows a fish of 12 inches (305 mm.) and since the Reeves illustrations were usually life-size, the British Museum specimen is probably not the model for the drawing. The illustration shows well the broad operculum characteristic of this species (Pl. 3, fig. 1). The lower third of the body is shown as dark bronze, the upper part silver—the reverse of what would be expected.

NOTE. Richardson identified this fish rather tentatively with Russell's Palasah and at the same time distinguished it from his own *Alosa reevesii* because of differences in head length, pectoral length and body outline. The specimen is clearly *H. reevesii* and not the Palasah of Russell (1803) (i.e. *Hilsa ilisha* (Ham. Buch.)—see Whitehead 1965*a*), having a broad operculum, its width contained only 1½ times in its length. The differences from *H. reevesii* noted by Richardson arise from a comparison of juveniles and adults and can be accounted for by allometric growth. Richardson records 40 scales in longitudinal series (42–45 in *H. reevesii* ; cf. 45–48 in *H. ilisha*—see Whitehead 1965*a*).

8. " ***Ilisha abnormis*** Gray "
= ***Ilisha elongata*** (Bennett)

Alosa elongata Bennett, 1830, *Mem. Life of Raffles* : 691.
Ilisha elongata: Norman, 1923, *Ann. Mag. nat. Hist.* (9) **11** : 7 (revision; Reeves' specimen examined) ; Fowler, 1930, *Proc. Acad. nat. Sci. Philad.* : 599 (Hong Kong) ; *Idem,* 1931, *Hong Kong nat.* **2** (2) : 121 (Hong Kong specimens).
Ilisha abnormis Richardson, 1846, *Ichth. China Japan* : 306.
Pellona vimbella Valenciennes, 1847, *Hist. Nat. Poiss.* **20** : 317 (specimen from Macao).
Pellona grayana Kner, 1865, *Reise Novara, Fische* : 328 (Hong Kong).

TYPE. A mounted skin (right side), 295 mm. standard length (total length about 14 inches, caudal tips damaged), *ex* China Seas, presented by J. R. Reeves. Hitherto unregistered, now BMNH. 1964.11.6.4. Underside of base of wooden stand marked " *Ilisha abnorma* H 240 R 81 ". The specimen is in poor condition, the anterior part of the flank lacking scales and having been sewn up across a large split in the skin and across the gill opening ; pectoral fin detached and sewn loosely to body ; a specimen of 14½ inches in British Museum (" dried and varnished ") mentioned by Richardson.

FIGURE. Reeves Nos. 81 and 67 are respectively a little larger and a little smaller than the type specimen. Both are recognizably *I. elongata* (Pl. 3, figs. 2 and 3). Detail of head poor in both illustrations.

NOTE. From the keys and descriptions given by Norman (1923) and Chu & Tsai (1958), there is no doubt regarding the identity of the type specimen, assuming of course that Richardson's counts were reasonably accurate. Unfortunately, scale and scute counts are no longer possible. Three other species are reported from China. *I. indica* (Swainson) is a deeper-bodied fish (depth 2⅗–3⅕ in length ; cf. 3⅘ in the type of *I. abnormis*) with 39–45 scales in lateral series (50–55 in *I. elongata*, and " about fifty scales " described by Richardson in the holotype of *I. abnormis*).

A second possible species is *I. novacula* (Valenciennes), again a rather deeper-bodied species (3½ in length) with fewer scales (45). *I. brachysoma* (Bleeker) is also a deeper bodied species with fewer scales in lateral series (42–45). In all three cases, the more slender body in Richardson's specimen distinguishes it, even if the meristic counts are not completely accurate.

The names *Ilisha* and *abnormis* were created by Gray in an unpublished catalogue of British Museum specimens. This catalogue is not now in the Zoological Library of this museum, and appears to have been lost. It was a continuation from the " Chondropterygii " of Gray (1851).

REDESCRIPTION OF THE TYPE OF *ILISHA ABNORMIS*

Standard length : 295 mm.
Total length : 356 mm. or 14 inches (approx., caudal tips damaged).

	mm.	%S.L.
Body depth	76·0	25·8
Head length	67·8	23·0
Snout length	19·6	6·5
Eye diam.	16·0	5·4
Upper jaw l.	34·0	11·5
Lower jaw l.	36·1	12·2
Pectoral length	37·5	12·7
Pelvic length	11·4	3·9
Length of anal base	118·0	40·0
Pre-dorsal	150·5	51·0
Pre-pelvic	116·3	39·5
Pre-anal	177·5	60·0

Lower jaw strongly projecting, upper jaw with two supra-maxillae but no hypomaxilla, extending to middle of eye if mouth closed, but not reaching to articulation of lower jaw.

Dorsal with iv 15 rays, its origin equidistant between snout tip and caudal base. Pectoral i 15. Pelvic (rays damaged) shorter than eye, its base a little nearer to pectoral base than to anal origin. Anal with iii 45 rays, its origin under last dorsal ray. Scales—no count possible. Scutes, 21 pre-pelvic, no count possible on post-pelvic (Richardson gives 14 + 13, but evidently missed seven pre-pelvic scutes).

9. " **Chatoessus aquosus** Richardson "
=**Konosirus punctatus** (Schlegel)

Chatoessus punctatus Schlegel, 1846, *Fauna Japon. Poiss.*, pt. 5 : 240, pl. 109, fig. 1.
Nealosa punctata : Herre & Myers, 1931, *Lingnan Sci. J.* **10** (2 and 3) : 236 (3 Hong Kong specimens).
Konosirus punctatus : Whitehead, 1962, *Bull. Brit. Mus.* (*nat. Hist.*) *Zool.* **9** (2) : 100 (generic review).
Chatoessus aquosus Richardson, 1846, *Ichth. China Japan* : 307.

TYPE. A dried skin (left side) mounted on wood, 190 mm. standard length, *ex* China, presented by Reeves. Hitherto unregistered, now BMNH. 1964.11.6.5 The specimen is in poor condition : pectoral detached, dorsal and anal fins damaged, caudal entirely missing. On the reverse side it is marked " H 230 R 63 ". This is the only specimen mentioned by Richardson, who gives its length as 7¾ inches.

FIGURE. Reeves No. 63 shows a clupeoid with a filamentous last dorsal ray, but with a rather rectangular suboperculum (Pl. 4, fig. 1). No scutes are shown, and there are about 45 scales in lateral series. Either *Konosirus punctatus* or *Clupanodon thrissa* are possible, but it must be presumed that the figure agrees with the specimen.

NOTE. The specimen conforms to the diagnosis of the monotypic genus *Konosirus* (Whitehead 1962*a*, p. 100) in the following characters :

a. Last dorsal ray, although now broken, sufficiently stout to have been filamentous.

b. Suboperculum with (exposed) anterior and upper margins meeting at obtuse angle, posterior margin rounded (exposed part of suboperculum rectangular in *Nematalosa*).

c. Outer edge of dentary not strongly flared outwards.

d. Post-pelvic scutes 14 or more likely 15 (cf. 11–12 in *Clupanodon thrissa*).

REDESCRIPTION OF THE TYPE OF *CHATOESSUS AQUOSUS*

Standard length : 190 mm.

	mm.	%S.L.
Body depth	57·0	30·0
Head length	47·4	24·7
Snout length	9·7	5·1
Eye diam.	9·3	4·9
Upper jaw l.	15·0	7·9
Lower jaw l.	19·0	10·0
Pectoral l.	33·0	17·4
Pelvic l.	17·0	8·9
Pre-dorsal	92·9	48·7
Pre-pelvic	97·2	51·1
Pre-anal	146·2	78·0

Dorsal with iii 14 (or iv 13) rays, its origin slightly nearer to caudal base than to snout tip. Pectoral with i 14 rays. Pelvic with i 7 rays, its base below first unbranched dorsal ray, and slightly nearer to pectoral base than to anal origin. Anal (count impossible) moderate, its base slightly longer than dorsal base, about 1¼ in head length. Caudal missing.

Scutes, 19 pre-pelvic, 15 post-pelvic (about 15 + 13 according to Richardson). Scales in lateral series, about 43 or 44 (Richardson, 46).

In all other features (jaws, opercular bones, etc.) this specimen conforms to the diagnosis for *Konosirus* given by Whitehead (1962*a*, p. 100).

The priority of Richardson's *aquosus* over Schlegel's *punctatus* need not be adhered to since the former is a *nomen oblitum* and there would be little value in resurrecting the name.

10. " **Chatoessus triza** Linnaeus "
= **Clupanodon thrissa** (Linnaeus)

[*Mystus altus* Linnaeus, 1754, *Chinensia Lagerströmiana*—" *dissertatio* " : 26—China, on Lagerström.]

[*Clupea thrissa* Osbeck, 1757, *Dagbok Ostind. Resa* : 257—Canton area.]

Clupea thrissa Linnaeus, 1758, *Syst. Nat.*, ed. 10 : 318 (name from Osbeck ; diagnosis after Lagerström).

Clupanodon thrissa: Fowler, 1930, *Proc. Acad. nat. Sci. Philad.* : 590 (Hong Kong) ; *Idem*, 1931, *Hong Kong Nat.* **2** (1) : 76 (Hong Kong specimens) ; Herre, 1934, *Hong Kong Nat. Supplement*, No. 3 : 26 (3 Hong Kong specimens) ; Whitehead, 1962, *Bull. Brit. Mus. (nat. Hist.) Zool.* **9** (2) : 100 (generic review).

Clupea triza Linnaeus, 1759, *Amoen. Acad.* **4** : 251.
Chatoessus triza: Richardson, 1846, *Ichth. China Japan* : 307 (on Reeves illustration, Canton or Macao).
Chatoessus maculatus Richardson, 1846, *Ichth. China Japan* : 308 (specimen from Canton).
Chatoessus osbeckii Valenciennes, 1848, *Hist. Nat. Poiss.* **21** : 106.

SPECIMENS. None are mentioned by Richardson and there are no Reeves specimens in the British Museum.

FIGURE. Reeves No. 224 shows a fairly deep fish (deeper than the preceding species), with an elongated last dorsal ray, a slender maxilla reaching almost to eye centre, and a dentary which is barely flared (Pl. 4, fig. 2). Mouth shape clearly eliminates *Nematalosa*, and two possibilities remain, the monotypic genera *Konosirus* and *Clupanodon*.

The illustration can be definitely identified on three characters.

a. *Snout.* The snout is less pointed than in the preceding figure (Pl. 4, fig. 1) and is a fair representation of the blunter snout found in *C. thrissa* compared with that in *K. punctatus*.

b. *Operculum.* In *C. thrissa* the operculum is slightly broader than in *K. punctatus* and its lower edge is a little higher up on the body. Although the opercular series in Reeves' drawings 63 and 224 are not completely accurate, yet the overall impression gives a good illustration of the differences in opercular shape between the two genera (compare Pl. 4, figs. 1 and 2).

c. *Anal base.* Again the artist has not made an accurate drawing, but the longer anal base in Reeves No. 224 (just over head length ; about head length or a little less in specimens of *C. thrissa*) can be contrasted with that shown in Reeves No 63 (about $\frac{4}{5}$ of head in both figure and in specimens of *K. punctatus*).

In addition, Reeves' illustration No. 224 shows a slightly deeper fish than in the illustration of *K. punctatus* (No. 63). *C. thrissa* is indeed a slightly deeper fish (depth $2\frac{2}{3}$–3 in standard length ; cf. 3–$3\frac{1}{2}$ in *K. punctatus* according to Regan, 1917*a*).

There can be little doubt, therefore, that the illustration refers to *C. thrissa* and not to *K. punctatus*, although Reeves himself was apparently dissatisfied with the painting. In his notes (list of illustrations, dates, etc.—see section on Reeves' illustrations), he states " 7th June [1828] Clupea sp. now transparent as glass –this badly painted."

NOTE. Richardson took the name *triza* from Linnaeus' *Chinensia Lagerströmiana* (1759), not from the *Systema Naturae* (1758), but that was incorrect. The earliest names, *Mystus altus* L., as well as *Clupea thrissa* Osbeck, were inadmissible (*Int. Code Zool. Nomen.* 1961, Art. 3).

The synonymy is cited here because the species was largely based on Osbeck's good description which was written (in November 1750) after examining (a) specimen(s) from the Canton area. In the two Lagerström descriptions by Linnaeus there is no mention of a filamentous last dorsal ray, but this is given in the *Systema Naturae*, presumably on Osbeck's description (" quorum ultimo duplo longior "). Lönnberg (1896) was able to identify a specimen of *Clupea triza* from the Lagerström collection at Uppsala ; he too, does not mention the filamentous last dorsal, which was presumably broken off.

11. "*Chatoessus chrysopterus* Richardson" = *Nematalosa sp.*, ? *N. nasus* (Bloch)

Clupea nasus Bloch, 1795, *Nat. Ausl. Fische*, **9** : 429, fig. 1.
Nematalosa nasus : Herre, 1934, *Hong Kong Nat. Supplement*, No. 3 : 26 (1 Hong Kong specimen).
? *Chatoessus chrysopterus* Richardson, 1846, *Ichth. China Japan* : 308 (on Reeves' illustration—Canton or Macao).
Konosirus thrissa : Jordan & Seale, 1905, *Proc. Davenport Acad. Sci.* **10**: 2 (Hong Kong) (*non Clupea thrissa* L.).

SPECIMENS. None mentioned by Richardson and no Reeves specimens in British Museum.

FIGURE. Reeves No. 61 shows a deep-bodied fish (depth $2\frac{1}{2}$ in standard length) with an elongated last dorsal ray and an inferior mouth with a short maxilla (Pl. 4, fig. 3). This is clearly a species of *Nematalosa*, and three species can be considered, *N. nasus*, *N. japonica* Regan and *N. come* (Richardson). There are two principle features shown in the illustration which may help to identify this drawing.

a. *Body depth :* the body shape shown in the illustration strongly suggests *N. come* (depth 2–$2\frac{1}{2}$ in length according to Regan, 1917*a*). In *N. japonica*, a more slender species judging from the type specimens in this museum, the depth is contained 3 times in length and the head $1\frac{1}{2}$ times in body depth ($1\frac{3}{4}$ in the illustration). *Nematalosa nasus* is also rather deep-bodied (depth $2\frac{2}{5}$–$2\frac{4}{5}$ times in length according to Regan, 1917*a*).

b. *2nd suborbital :* in the illustration, the anterior border of the 2nd suborbital is shown as slightly oblique (rather than vertical) and the edge is concave (rather than straight or convex). In *N. nasus* alone, the anterior border is vertical and slightly convex (see Whitehead, 1962*a*, fig. 4). In all other species the anterior border is oblique, and leaves exposed a small triangular area above the anterior part of the lower limb of the pre-operculum. Such a naked area is not, however, shown in the drawing.

NOTE. *Nematalosa japonica* can be eliminated because of its more slender body. The only record of *N. japonica* from the Hong Kong area seems to be the single specimen examined by Herre & Myers (1931). The Reeves figure probably best fits *N. come*, but this species is not known from so far north (Indo-Australian Archipelago according to Regan). It differs from *N. japonica* in having a deeper body and a lower scute count (11–14 post-pelvic scutes ; cf. 13–16—see Whitehead, 1962*a*), but a more strongly flared dentary. Unfortunately, neither of these two features can be determined from the drawing. Finally, it must be wondered whether Richardson would not have recognized his own species (i.e. *N. come*), especially since he comments on the close correspondence between the ichthyofauna of the northern and southern parts of the western shores of the Pacific (" Report ", p. 190).

Nematalosa nasus, the remaining possibility, is recorded from the Philippines, China and Japan, and two Hong Kong references appear in the literature (see synonymy). There is a Hong Kong specimen in this museum. The discrepancy in shape of 2nd suborbital might be misinterpretation by the artist, for certainly the dermal head bones are not accurately drawn in any of the drawings. A mistake of this kind seems much more likely than one in body depth, and the drawing agrees with *N. nasus* and not with other species of *Nematalosa* in failing to show the small naked, triangular area above the anterior part of the pre-operculum. *Nematalosa nasus* is therefore chosen as the most likely species.

12. " ***Chatoessus maculatus*** Gray "
= ***Clupanodon thrissa*** (Linnaeus)

(see synonymy under *Chatoessus triza.*)

Specimens. Richardson states that a single specimen was presented by Vachell to the Cambridge Philosophical Institution. There is now no such specimen in the Cambridge collections, and Günther (1868, p. 409) does not list any Vachell material for this species. In 1893, S. F. Harmer, then director of the Museum in Cambridge, listed all fish specimens, but *C. maculatus* does not appear on the list.[1] It may have been one of the specimens destroyed in 1866, during the overhaul of the collections. An account of the Vachell collection is given by Whitehead (in press).

Günther (loc. cit.) listed three specimens of *C. maculatus* collected by Swinhoe from Formosa; these are *Clupanodon thrissa*. Richardson believed *C. maculatus* to be close to *C. chrysopterus*, both sharing the same Chinese vernacular name, but the Reeves figure (Pl. 5, fig. 1) shows upper and lower jaws typical of *Clupanodon*.

Figure. According to the Reeves notebook, this figure was painted at Canton in November 1828. Reeves notes 6 or 7 black spots on the flanks, and these are well shown in Reeves No. 109 (Pl. 5, fig. 1). But for the elongated last dorsal ray, this figure resembles *Hilsa kelee* (Cuvier). Apart from the spots it is otherwise similar to the figure of *C. triza* (Reeves No. 224, see Pl. 4, fig. 2).

Notes. The name *maculatus* was first used by Gray in a manuscript list of fishes in the British Museum. As in the case of other manuscript names (by Forster and one by Broussonet), Richardson accredited the name to Gray even though the list had not been published. As stated earlier, this list never was published and now appears to be lost.

13. " ***Engraulis commersonianus*** Lacepède "
= ***Stolephorus commersonii*** Lacepède

Stolephorus commersonii Lacepède, 1803, *Hist. Nat. Poiss.* **5** : 381, 382, pl. 12, fig. 1.

Engraulis commersonianus : Richardson, 1846, *Ichth. China Japan* : 308 (Reeves specimens *ex* " China ") ; Fowler, 1930, *Proc. Acad. nat. Sci. Philad.* : 600 (Hong Kong, as *commersonii*).

Engraulis japonica : Günther (*part.*), (*non E. japonica* Schlegel) 1868, *Cat. Fish. Brit. Mus.* **7** : 390 (Reeves specimens *ex* " China ").

Engraulis chinensis Günther, 1880, *Rep. Voy. Challenger*, **1** : 73 (Reeves specimens and 4 other Chinese specimens—see below).

Specimens. Four fishes, 79–82 mm. standard length, *ex* China, presented by J. R. Reeves, hitherto labelled " *Engraulis japonica* " and unregistered, now BMNH.

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[1] Harmer's Catalogues (two manuscript volumes) are now in the University Museum of Zoology in Cambridge.

1964.11.6.8.11. These are the specimens listed as c–f in Günther's Catalogue (1868, p. 390). All are in good condition. For reasons given below, these fishes should not be regarded as syntypes of *Engraulis chinensis* Günther, 1880.

FIGURE. There is no Reeves figure of this species.

NOTES. As a result of the poor description given by Houttuyn (1782) of a species, *Atherina japonica* (variously interpreted as one of two species of anchovy or a species of round herring—see Whitehead, 1963*b*), considerable confusion existed in the nomenclature of the Chinese and Japanese anchovies. However, Richardson correctly identified the British Museum specimens with Lacepède's *Stolephore commersonien.* Richardson noted that Cuvier had ranged the latter species " among the anchovies, whose bellies are not toothed " (i.e. the modern genus *Engraulis*). But he observed that the Reeves specimens " show six teeth before the ventrals as fine hairs " (characteristic of the modern genus *Stolephorus*). Unfortunately, Richardson placed *Atherina australis* Shaw (a true member of *Engraulis*—Whitehead, 1964*b*) in his synonymy of *E. commersonianus.*

Günther (1868, p. 390), overlooking Schlegel's *Engraulis japonica* (a true *Engraulis*), placed the Reeves specimens and some further Chinese specimens in *Engraulis japonica* (Houttuyn). Later (Günther, 1880), finding a difference in finray counts between his *E. japonica* and Schlegel's, he proposed the name *Engraulis chinensis* for the Reeves and other specimens. These specimens appear in Günther's catalogue (1868, p. 390) as:

a, b, c–f Adult and half grown China
g–i Adult. Amoy. Purchased of Mr. Stevens

Specimen a is registered BMNH. 1831.12.27.207. It is now an alizarin preparation (standard length 60 mm.). Specimen b is a juvenile (46 mm. S.L.) ; it is *Engraulis japonicus* Schlegel and was evidently misidentified. Specimens c–f are labelled " J. R. Reeves " but it is not clear why Günther did not record them as such. Specimens g–i are registered BMNH. 1860.7.20.103.6.

Since the Reeves specimens are not positively identified as such in Günther's catalogue, it seems best to regard the three Stevens specimens as the syntypes of *Engraulis chinensis* Günther (four fishes registered but one missing).

Fowler (1931, p. 199 ; 1941, p. 695) included *Engraulis commersonianus* of Richardson in his synonymy of *Engraulis japonicus* Schlegel, overlooking Richardson's reference to abdominal scutes. However, *E. japonicus* certainly occurs in the Philippines and is also found in Hong Kong waters (B.M. specimens). Closely related to *S. commersonii* is *S. indicus* (van Hasselt), reported by Seale (1914) and Herre & Myers (1931) from Hong Kong. The latter species can be distinguished from *S. commersonii* chiefly by its shorter maxilla (to front edge of operculum, not to gill-opening). Fowler (1931, p. 201) lists only one other Chinese record for *S. indicus*, namely *Engraulis encrasicholus* of Günther (1874) from Chefoo. However, these Günther specimens (collected by Swinhoe) are true *Engraulis japonicus*. *Stolephorus indicus* is well known in the Philippines, and is reported from Formosan and Japanese waters (Hayashi & Tadokoro, 1962). I have examined five Hong Kong specimens of *S. indicus* deposited in the Zoologiske Museum in Copenhagen (Nos. 99–101).

14. " *Coilia grayii* Richardson "
= *Coilia mystus* (Linnaeus)

[*Mystus ensiformis* Linnaeus, 1754, *Chinensia Lagerströmiana*—" *dissertatio* " : 26, fig. 12—China, on Lagerström.]

[*Clupea mystus* Osbeck, 1757, *Dagbok Ostind. Resa* : 256—Canton area.]

Clupea mystus Linnaeus, 1758, *Syst. Nat.*, ed. 10 : 319 (name from Osbeck ; description mostly after Lagerström) ; *Idem*, 1759, *Amoen. Acad.* **4** (61) : 252, fig. 12 (repeat of 1754 description and figure.)

Coilia mystus : Jordan & Seale, 1926, *Bull. Mus. Comp. Zool.* **67** (11) : 359 (Hong Kong) ; Fowler, 1931, *Hong Kong Nat.* **2** (3) : 206 (China, compiled) ; Herre, 1934, *Hong Kong Nat. Supplement*, No. 3 : 26 (2 Hong Kong fishes).

Coilia grayii Richardson, 1845, *Ichth. Voy. Sulphur* : 99, pl. 54, figs. 1–2 (China seas) ; *Idem*, 1846, *Ichth. China Japan* : 309 (on type and Reeves illustr.) ; Jordan & Seale, 1926, *Bull. Mus. Comp. Zool.* **67** (11) : 361 (4 Hong Kong specimens) ; Herre & Myers, 1931, *Lingnan Sci. J.* **10** (2–3) : 238 (4 Hong Kong specimens).

TYPE. A fish, 243 mm. standard length (about 10½ inches in total length, caudal tip damaged), registered BMNH. 1855.9.19.1581, presumed *ex* China Seas, sent to British Museum from the Haslar Hospital Museum to which (*fide* Richardson 1844, p. 100) it had been presented by Captain Dawkins, R.N. Although this specimen was listed as type by Günther (1868, p. 405), the jar containing it (with original label) has not been marked as containing a type. Instead a second jar has been labelled *C. grayii* TYPE. This jar contains two smaller specimens, also from the Haslar collection, registered BMNH. 1855.9.19.1157. Richardson (1844) clearly states the length of the specimen from which the description was made (11 inches) ; his plate (pl. 54, fig. 1), stated to be life size, shows a fish of 250 mm. standard length. The two smaller Haslar specimens are barely 7½ inches.

SPECIMENS. Günther (loc. cit.) lists five specimens under *C. grayii*. The first, indicated as " *a* ", is the type ; *b*, is an adult (in alcohol) presented by J. R. Reeves ; *c* is another adult (stuffed) also presented by J. R. Reeves but subsequently destroyed; *d* and *e* are the two small Haslar specimens. Curiously enough, Richardson does not mention these Reeves specimens, although the old label on the jar of the surviving (alcohol) specimen has the Hardwicke illustration number on it (H 252 R). This fish, 235 mm. standard length, is now registered BMNH. 1964.11.6.2.

FIGURE. Reeves No. α14 (13½ inches total length) shows a species with seven filamentous pectoral rays and a blunt maxilla reaching only to the pectoral base (Pl. 5, fig. 2). However, the maxilla has the appearance of having been broken off at its tip. Although the finrays of the anal and caudal are shown (correctly) as contiguous, the two fins are strongly demarcated by colour (anal grey/green, caudal orange/yellow). Scales and scutes are rather vaguely shown, and the drawing is far inferior to that given in the *Voyage of the Sulphur* (Richardson, 1844, pl. 54, fig. 1). The surviving Reeves specimen, of 10¼ inches, is too small to have been model for the Reeves illustration.

NOTE. This is the second of the two clupeoid species listed by Osbeck (1757), and reference is made to this early description in the synonymy since it was based on a Canton record and was used by Linnaeus (1758) in describing the species. Linnaeus

(1754) had originally named this fish *Mystus ensiformis*, giving a figure (fig. 12) which was later reproduced in the *Amoenitates Academiae* (1759). As in the case of *Mystus altus*, Linnaeus evidently decided to give priority to the name used by his pupil Osbeck during the latter's voyage in 1770, although that name did not appear in print until 1757.

The genus *Coilia* is badly in need of revision. It is not known, for example, to what extent small variations in numbers of pectoral filaments or gillrakers truly indicate specific differences. Authors have been divided on whether *C. grayii* is a distinct species or whether it is conspecific with *C. mystus*. Fowler (1931) distinguished the two on gillraker counts (*C. mystus* 22–25 ; *C. grayii* 28–30) and anal rays (70–86 and 86–92 respectively), but later (Fowler, 1941) he increased the range of anal rays in *C. mystus* to include *C. grayii*. Lönnberg (1896) identified a specimen at Uppsala (labelled *Clupea encrasicolus* Mus. Lin.) as the type of *C. mystus*, claiming that it was really one from the Lagerström collection which had been mislabelled. Lönnberg gave no gillraker count (if such a count is indeed possible), but on pectoral filament numbers placed *C. grayii* in the synonymy of *C. mystus* (7 free filaments) ; he distinguished *C. clupeoides* Lacepède (with 6 free filaments) as a separate species. It can be noted, however, that Lacepède (1803, pp. 466, 467) does not refer to filamentous pectoral rays and based his description on *Clupea mystus* of Linnaeus and Osbeck. The single specimen of *C. mystus* of Jordan & Seale (1926, p. 359) had 6 free pectoral rays and 24 gillrakers. Günther (1868) and Fowler (1941) list *C. clupeoides* as a synonym of *C. mystus*. The status of those species with only 6 pectoral filaments is discussed under the next species.

REDESCRIPTION OF TYPE AND REEVES SPECIMEN

TYPE : BMNH. 1855.9.19.1581 ; Reeves fish : BMNH. 1964.11.6.2.
Standard length : 243 mm. (TYPE) ; 238 mm. (Reeves)
Total length : 275 mm. (TYPE) ; 262 mm. (Reeves)

	mm.		%S.L.	
Body depth	45·2	41·3	18·5	17·3
Head length	44·2	40·2	18·1	16·9
Snout length	9·6	9·1	3·7	3·8
Eye diam.	8·9	8·6	3·6	3·6
Upper jaw l.	54·3	51·1	21·9	21·5
Lower jaw l.	30·8	29·6	12·7	12·4
Pectoral l.	79·5	88·2	32·7	37·0
Pelvic l.	19·4	15·9	8·0	6·7
Pre-dorsal	73·7	65·4	30·2	27·4
Pre-pelvic	69·2	66·0	28·5	27·7
Pre-anal	105·0	100·2	43·0	42·0

Body compressed, depth about equal to head length, posterior portion elongated, caudal peduncle about $\frac{3}{4}$ eye at caudal base. Maxilla pointed posteriorly, reaching well beyond pectoral base, with fine conical teeth in a single series along entire lower edge becoming larger posteriorly ; two supramaxillae. Fine teeth present on premaxillae, vomer, pterygoids, palatines and on dentaries, the latter with well-developed coronoid process. Pseudobranch exposed, almost equal in length to eye diameter, filaments about twenty, short.

Dorsal (preceded by small spine) with iii 10 rays. Pectoral with vii 10 rays, the first seven filamentous and unbranched, reaching to about base of 10–14th branched anal ray, well beyond tip of depressed dorsal ; branched rays of pectoral reaching beyond pelvic base. Pelvic i 6, its base below anterior dorsal rays and nearer to pectoral base than to anal origin. Anal iii 88 and iii 86, final rays joined to lower rays of caudal.

Scales caducous, no count possible. Abdominal scutes trenchant, 12 and 15 pre-pelvic, 24 and 24 post-pelvic, the latter with slender ascending arms, alternately long and short.

Gillrakers moderate, about eye diameter, strongly armed with serrae along inner edge ; 22 and 22 rakers on upper arm of 1st arch, 30 and 27 on lower arm.

Branchiostegal rays 11.

15. " ***Coilia playfairii*** McClelland "
= ***Coilia playfairii*** (McClelland)

Choetomus playfairii McClelland, 1844, *Calcutta J. nat. Hist.* **4** : 405, pl. 24, fig. 3 (China on Playfair specimen(s)).

Coilia playfairii : Richardson, 1845, *Voy. Sulphur Ichth.* : 100, pl. 54, figs. 3–4 (Hong Kong, China seas) ; *Idem*, 1846, *Ichth. China Japan* : 309 (Japanese specimen).

Coilia grayi Kner, 1865, *Reise Novara, Fische* : 335 (Hong Kong).

Coilia clupeoides : Günther (*part.*), 1868, *Cat. Fish. Brit. Mus.* **7** : 404 (Richardson specimen *ex* China).

Coilia nasus: Günther, 1868, *Cat. Fish. Brit. Mus.* **7** : 405 (Japanese, Chinese specimens) ; Nichols, 1943, *Nat. Hist. Central Asia,* **9** : 19 (Anhwei, nr. Canton).

? *Coilia ectenes* Fowler, 1930, *Proc. Acad. nat. Sci. Philad.* : 601 (Hong Kong) ; *Idem*, 1931, *Hong Kong Nat.* **2** (3) : 208 (Kong Hong specimens).

SPECIMENS. No Reeves specimens listed by Richardson and none in British Museum collections. There is, however, a Japanese specimen (173 mm. standard length, labelled " Adara Japan ") which Richardson states was " labelled ' Adara ' by the authors of the ' Fauna Japonica ' ". This fish was identified by Günther (1868, p. 406, specimen " a ") as *C. nasus*. There is also a Chinese specimen (150 mm., BMNH. 1847.5.10.5) presented by Richardson which Günther (loc. cit., p. 404) included under *Coilia clupeoides* Lacepède. The jar was later marked " *Coilia playfairii* TYPE ". In fact this specimen may well be that on which the figure of *C. playfairii* in the " Voyage of the Sulphur " was based (pl. 54, fig. 3, stated to be natural size). However it is not a type. Finally, there is a Vachell fish of 268·5 mm. S.L. at Cambridge (Whitehead, in press).

FIGURE. Reeves No. β26 shows a smaller fish than the figure for *C. grayii*, with a steeply rising dorsal profile (Pl. 5, fig. 3). The drawing is poor compared to that given in the " Voyage of the Sulphur ". The number of pectoral filaments shown is 6.

NOTE. Several nominal species of *Coilia* are stated to have 6 (or 5–6) free filamentous pectoral rays. Excluding those with pearly spots along the flanks (light organs, see Haneda, 1961), or with few post-pelvic scutes (9–11), or a short maxilla not reaching the gill opening, there are three species known from Chinese or Japanese waters (*C. playfairii*, *C. nasus* and *C. ectenes*). Jordan & Starks (1906) and Jordan & Herre (1906) distinguished *C. ectenes* Jordan & Seale from *C. nasus* Schlegel mainly because of its greater number of anal rays and abdominal scutes and its more elongate form. The Japanese specimen labelled " Adara " (see above) has a markedly elongate body compared with other Chinese or Japanese specimens examined, and it has 49 scutes (48–49 in *C. ectenes :* cf. 42–43 in *C. nasus*, according to Jordan & Starks, 1906), and 90 anal rays (96–113 in *C. ectenes* ; cf. 80–82 in *C. nasus*). However, Boeseman (1947, p. 178) describes 46 scutes and 85–88 anal rays in the type material of *C. nasus*, while Richardson (1844) gives 42–47 scutes and 70–80 anal rays for *C. playfairii*.

Thus the meristic differences separating these three nominal species are slight, and further material may well show that only a single small species is present in Chinese and Japanese waters, viz. *C. playfairii*. Fowler (1941) placed all three in the synonymy of *C. mystus*, but the latter differs in pectoral count and, on the basis of the specimens in the British Museum, appears to be a larger species. As noted already, Jordan & Seale (1926) found 6 pectoral filaments and 24 gillrakers in the specimens they considered to be *C. mystus* ; they record 7 filaments and 30 gillrakers in their specimens of *C. grayii*.

16. " ***Thryssa mystax*** Bl. Schn."
= ***Thryssa mystax*** (Schneider)

Clupea mystax Schneider, 1801, *Syst. Ichth. Bloch.* : 426, pl. 83 (Malabar).
Thryssa mystax : Richardson, 1846, *Ichth. China Japan* : 309 (on Reeves specimens).
Engraulis mystax : Fowler, 1930, *Proc. Acad. nat. Sci. Philad.* : 600 (Hong Kong).
Setipinna mystax : Fowler, 1931, *Hong Kong Nat.* **2** (3) : 203 (Hong Kong specimens).
Engraulis hamiltonii : Günther, 1868, *Cat. Fish. Brit. Mus.* **7** : 395 (Reeves and other Chinese specimens).

SPECIMENS. A fish, 183 mm. standard length (in alcohol) *ex* China presented by J. R. Reeves, with a metal tag sewn to caudal peduncle " R 138 " ; jar labelled " Clupea H 236 306 R 138 ", hitherto unregistered, but now BMNH. 1964.11.6.12. There is also a mounted skin (left side), labelled " *Engraulis hamiltonii* China J. R. Reeves, Esq." and with the Hardwicke and Reeves illustration numbers pencilled on the wooden base ; hitherto unregistered, now BMNH. 1964.11.6.13. Both specimens are mentioned by Richardson.

FIGURE. Reeves No. 138 might well have been drawn from the dry specimen in this museum, being only slightly larger than the illustration. It shows a rather deep-bodied compressed engraulid with post-pelvic scutes, a maxilla reaching beyond the posterior margin of the operculum, a long anal fin and no filamentous pectoral rays (Pl. 6, fig. 1). The black venulose supra-scapular area seen in the specimens is clearly shown in the illustration[1], and the position of the fins closely correspond with those in the dried specimen. Richardson notes " an indistinct stripe along the middle of the anal ", but this does not appear in the preserved material.

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[1] Referred to as " hairy process behind gills " in the Chinese Chrestomathy under species No. 4 (Bridgman 1841, p. 480).

NOTE. Fowler (1931) recorded both *T. hamiltonii* and *T. mystax* from Hong Kong. *T. hamiltonii* is distinguished from *T. mystax* by its shorter maxilla (to gill opening or just beyond; cf. to or beyond pectoral base in *T. mystax*). It is suspicious, however, that the specimens of *T. hamiltonii* in our collections are mostly large fishes, whereas those of *T. mystax* are small. Amongst the smaller specimens labelled *T. hamiltonii* (100 mm. and below), the maxilla reaches almost to the pectoral base. In all other respect these two nominal species are similar and their meristic counts overlap. The genus is currently under revision by Dr. S. Dutt.

The name *Thrissocles* Jordan & Evermann, widely but wrongly used for this genus as a senior synonym, should be replaced by *Thryssa* Cuvier, 1829 (see Whitehead, 1965*b*). Fowler (1931, p. 203) placed both *T. mystax* and *T. hamiltonii* in *Setipinna* Swainson, although he had (correctly) characterized that genus as possessing a filamentous upper pectoral ray.

DESCRIPTION OF REEVES SPECIMENS

Standard lengths: 183 mm. BMNH. 1964.11.6.12 (alcohol)
188 mm. BMNH. 1964.11.6.13 (skin)
(Figures for the alcohol specimen are given first.)

	mm.		% S.L.	
Body depth	46·4	51·2	25·3	27·3
Head length	40·1	41·7	22·0	22·3
Snout length	5·8	7·2	3·2	3·8
Eye diam.	8·6	8·6	4·7	4·6
Upper jaw length	41·5	41·7	22·7	22·3
Lower jaw length	30·5	29·5	16·7	15·7
Pectoral l.	32·2	—	17·6	—
Pelvic l.	13·8	—	7·5	—
Anal base l.	54·1	63·8	29·6	33·8
Pre-dorsal	95·4	102·9	52·2	54·5
Pre-pectoral	43·9	—	24·0	—
Pre-pelvic	75·4	—	41·5	—
Pre-anal	115·9	122·5	63·5	65·5

Body compressed, its width almost three times in its depth. Maxilla long, reaching beyond posterior border of operculum to a point half way between operculum border and base of first pectoral ray. Pectoral fins just reaching base of pelvics, the tips of the latter just before dorsal origin. The following counts apply to the alcohol specimen only.

Dorsal with iii 11 rays, preceded by a minute spine, its origin equidistant between caudal base and anterior half of eye. Pectoral i 10; pelvic i 6. Anal with iii 37 rays, its origin slightly behind last dorsal ray.

Abdominal scutes keeled, with sharp spines, 18 pre-pelvic (first minute), 11 post-pelvic (Richardson, 13 + 9).

Gillrakers 9 + 14 on first arch, each raker bearing serrae of approximately even length, not ranged into clumps.

Scale counts not possible (Richardson, 38).

Venulose supra-scapular area with the venules dotted with small, linearly arranged melanophores. Flanks silver, except for upper $\frac{1}{6}$ which is brown. All fins hyaline.

17. " ***Megalops setipinnis*** Forster "
= ***Megalops cyprinoides*** (Broussonet)

Clupea cyprinoides Broussonet, 1782, *Tableau Ichth.* : no pagination, pl. 9 (Oceans between the tropics).

Megalops setipinnis Richardson, 1843, *Ann. Mag. nat. Hist.* **11** : 493 (Port Essington) ; *Idem*, 1846, *Ichth. China Japan* : 310 (Seas of China).

Megalops curtifilis Richardson, 1846, *Ichth. China Japan* : 310 (on Reeves illustrations, Chinese Seas).

TYPE. A skin (right side), 180 mm. standard length, labelled " Fresh water swamp near Victoria, Port Essington " and on the reverse side " Sept. 20.1840.***3***.". A second label, pasted on the inside of the specimen, reads " 3. *Megalops setipinna* Forster." This is the smaller of two skins, the other of which is registered BMNH. 1853.1.4.20 ; both are listed by Günther (1868, p. 472, d–e).

Richardson (1842 and subsequent papers on Australian fishes) described some dried skins numbered 1–37, presented to this museum by J. Gould and collected in the Port Essington area by Gould's assistant, Gilbert. In the original description of *M. setipinnis*, Richardson (1843, p. 493) describes a single Gilbert specimen of 9 inches 2 lines total length, " No. 3, Mr. Gilbert's list ". The smaller of the two British Museum skins, although now with damaged caudal tips, corresponds with the measurements given by Richardson. This fish is certainly the holotype of *M. setipinnis* Richardson, 1843, and it is now registered BMNH. 1964.11.6.14.

SPECIMENS. Richardson states that he had seen no Chinese (or Indian) specimens, and there are no Reeves specimens in the British Museum. There are two alcohol specimens from Port Essington (BMNH. 1843.8.10.11 and 1855.9.19.1142–3). The first of these was presented by Gould and was no doubt one of those referred to by Richardson in the " Report ".

FIGURE. Reeves No. 96 is a fair illustration (Pl. 6, fig. 2), showing well the anastomising canals on the lateral line pore scales. There is, however, a single canine shown in the upper jaw ; Richardson remarks on this anomaly.

NOTES. Richardson based his name for this species on a pencilled title " *Clupea setipinna* " written underneath the uncoloured and only partly finished drawing by J. G. Forster (No. 242 in Forsters drawings from Cooks 2nd voyage, 1772–75, the 2nd of two volumes in the Zoological Library of the British Museum (Natural History)). Since Forster's drawings were unpublished, Richardson was wrong to place *Clupea cyprinoides* Broussonet, 1782 as a junior synonym of this species.

Amongst the drawings, figures, etc. belonging to Richardson and left to this museum by his son, there is a tracing of Forster's " Kundinga " with a pencilled note underneath " not Gilbert's fish ". In his description of *M. setipinnis* Richardson notes that the Reeves drawing corresponds " exactly in profile and size of fins, shape of head, etc." with the figures of both Forster and Broussonet, but that Forster's colours are different.

18. " *Megalops curtifilis* Richardson "
= ***Megalops cyprinoides*** (Broussonet)

(See previous species for synonymy.)

SPECIMEN. No specimens mentioned by Richardson, and none in British Museum.

FIGURE. Reeves No. 136 shows a smaller fish than in No. 96, but clearly referable to *Megalops cyprinoides* (Pl. 6, fig. 3). The dorsal filament is a little shorter and the upper jaw a little longer than in No. 96, but the pored lateral line scales with their radiating canals are well shown.

NOTE. This is evidently *M. cyprinoides*, the differences found by Richardson being attributable to poor drawing (scales fewer) and the fact that it was most likely a juvenile (dorsal filament shorter, body more slender).

19. " ***Elops machnata*** Forskål "
= ***Elops machnata*** (Forsskål)

Argentina machnata Forsskål, 1775, *Descriptiones Animal.* : 13, 68 (Red Sea).
Elops machnata : Richardson, 1846, *Ichth. China Japan* : 311 (Canton, Seas of China).
Elops purpurescens Richardson, 1846, *Ichth. China Japan* : 311 (Chinese Seas).
Elops saurus : Günther, (part), 1868, *Cat. Fish. Brit. Mus.* **7**: 470 (Reeves specimen, Indo-Pacific material).

SPECIMEN. Richardson states that Reeves deposited a specimen from Canton in this museum. Amongst the stuffed specimens is one, of 390 mm. standard length, originally labelled " *Elops saurus* " but with the name " *machnata* " added in another hand. Unlike the other stuffed Reeves specimens, no details are painted on the wooden base, but a pencilled note underneath reads " *Elops machnata* Canton J. R. Reeves Esq.". The specimen was hitherto unregistered but is now BMNH. 1964. 11.6.3.

FIGURE. Reeves No. 137 is a fair drawing and easily recognizable as *Elops* by its small scales, elongate body, pored lateral line scales, etc. (Pl. 7, fig. 1).

NOTES. The specimen has approximately 87 pored lateral line scales, which accords with *E. machnata*, and the lower jaw (now set open) probably covered the pre-maxillary tooth band when the jaw was closed (lower jaw included in *E. hawaiensis* Regan). On the basis of the most recent key (Whitehead, 1962*b*) the specimen is evidently *E. machnata*. Richardson rightly distinguished his fish from the *Mugil salmoneus* (Forster) Schneider figured in his Ichthyology of the Erebus and Terror (Richardson, 1896, pl. 36, figs. 1, 2) ; that fish was *Chanos chanos* (Forsskål), a species apparently not encountered by Reeves.

20. " ***Elops purpurescens*** Richardson "
= ***Elops machnata*** (Forsskål)

(See previous species for synonymy.)

TYPE. Richardson based this name solely on the Reeves illustration. The name is now a *nomen oblitum* but it is very unlikely that a distinct Chinese or Western Pacific species or subspecies of *Elops* will ever be recognized.

FIGURE. Reeves No. 53 appears to have been drawn from a specimen long out of water (Pl. 7, Fig. 2). The fins have darkened, the flanks are paler and the back is darker than in the figure of *E. machnata*. In addition, the body is twisted, giving a more convex lower profile than in the preceding species.

NOTE. Richardson distinguished this fish from *E. machnata*, but added " This drawing does not differ very greatly from the preceding one in form ". He notes its more irregular and less arched dorsal outline, more convex belly and slightly decurved lateral line. He also notes a slight difference in the Chinese names given by Reeves : *Chuh Keaou*, " Bamboo——" for *E. machnata* ; *Chuh Kin*, " variegated Bamboo " for *E. purpurescens*.

The figure suggests merely a twisted specimen of *E. machnata*. Only a single species of *Elops* is recognized from the Western Pacific (see Whitehead, 1962*b*).

21. " **Chirocentrus dorab** Forskål "
= **Chirocentrus dorab** (Forsskål)

Clupea dorab Forsskål, 1775, *Descriptiones Animal.* : 72 (Red Sea).

Chirocentrus dorab : Richardson, 1846, *Ichth .China Japan* : (Canton, seas of China) ; Günther, 1868, *Cat. Fish. Brit. Mus.* **7** : 475 (Reeves specimen) ; Fowler, 1930, *Proc. Acad. nat. Sci. Philad.* : 598 (Hong Kong) ; *Idem*, 1931, *Hong Kong Nat.* **2** (1) : 75 (Hong Kong specimens) ; Herre, 1931, *Hong Kong Nat. Supplement*, No 3 : 26 (2 Hong Kong specimens).

SPECIMEN. Richardson mentions an alcohol specimen from Canton presented by Reeves of 10¼ inches. This specimen (220 mm. S.L. ; hitherto unregistered, but now BMNH. 1964.11.6.1) is labelled " *Chirocentrus dorab* China J. R. Reeves Esq. H 237 R ". It lacks scales and the fins are damaged slightly, but otherwise the specimen is in fair condition.

FIGURE. As Richardson noted, the Reeves figure (Reeves No. 47) hints at pungent ventral scutes (Pl. 7, fig. 3), but these spines are in fact the tips of the ribs, a common artifact in preserved specimens of *Chirocentrus*. The figure shows no scales, but it is not possible to judge whether the present specimen (10¼ inches) served as model for the illustration (15 inches).

NOTES. This specimen has 5 + 16 gillrakers on the first arch, a count which places it in *C. hypselosoma* Bleeker according to Hardenberg (1930) (modal count 14–15 on lower part of first arch for *C. dorab*). On the other hand, the body depth is contained 6 times in standard length in the Reeves specimen and the maxilla does not reach the front border of the preoperculum, which accords with *C. dorab* (5½ and beyond respectively in *C. hypselosoma*). The systematic position of Bleeker's *C. hypselosoma* has been examined elsewhere (Whitehead, Boeseman & Wheeler, in press) and the conclusion reached that there may indeed be two species of *Chirocentrus* present in the Indo-Pacific. However, for the present, the Reeves fish is identified with *C. dorab* until the two species can be more trenchantly defined.

LIST OF HONG KONG ELOPOID AND CLUDEOID SPECIES

For a list of the elopoid and clupeoid species recorded from the Hong Kong area (see Table 2) I have relied chiefly on Fowler (1930, 1931), Herre & Myers (1931) and Herre (1934). There have been few subsequent records. In addition to published records, the list of species given has been augmented by inclusion of specimens represented in the British Museum collections, and especially by Hong Kong specimens generously donated to the museum by Mr. W. Chan.

Hong Kong lies just within the tropics, and many of the species found there are common both to the Philippines and to the sea around Taiwan (Formosa). Where species have been reported from near Taiwan (Chen, 1961, and a useful review of clupeoids by Chu & Tsai, 1958), or from Korea (Mori, 1952), or from Japan (Matsubara, 1955), and at the same time are also known from the Philippines (Fowler, 1941 ; Herre, 1953), then I have assumed their probable occurrence in Hong Kong waters. Such an assumption is usually justified in clupeoid fishes, the marine species, at least in the Indo-Pacific region, being for the most part wide-ranging.

Forty-four species are listed here, more than twice as many as were known to Richardson. However, in eleven cases there is no actual Hong Kong record or specimen, and the list for certain genera can only be tentative. This is particularly true for the genera *Herklotsichthys* and *Sardinella*. The species of *Stolephorus* of this area are also poorly known, but the Chan collection contained three species and showed, perhaps surprisingly, that one of the commonest is *S. buccaneeri* Strasburg, a species closely related to *S. purpureus* Fowler, both of which were believed confined to the Hawaiian Islands. The presence of *S. buccaneeri* in the Hong Kong region may explain the reports of *S. zollingeri* (Bleeker) from Japanese waters (Hayashi & Tadokoro, 1962). Thus the types of *S. zollingeri* are not members of *Stolephorus* at all, but are *Engraulis japonicus* Schlegel (Whitehead, 1964*b*), a species unlikely to be misidentified by Japanese workers. But published descriptions of *S. zollingeri* in Japanese waters (e.g. Hayashi & Tadokoro, loc. cit.) strongly suggest *S. buccaneeri*, although none have mentioned the characteristic diamond-shaped urohyal plate (see Whitehead, 1965*b*, fig. 4a). Specimens of *S. buccaneeri* have also been recorded from the Red Sea region and from Durban (Whitehead, 1965*b*) but not from intervening areas.

The list of species of *Thryssa*, *Coilia* and *Ilisha* given here must also be considered tentative, all three genera badly needing revision.

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Table 2

Elopoid and clupeoid species recorded from the vicinity of Hong Kong.

Species	Reference
Elopidae	
Elops machnata (Forssk.)	Richardson, 1846 (Canton*).
Megalopidae	
Megalops cyprinoides (Brouss.)	Richardson, 1846 (on Reeves Illustr.)
Albulidae	
†*Albula vulpes* (Linn.)	[Fowler, 1941—Japan, East Indies; Liu & Shen, 1957—Taiwan.]
Chirocentridae	
Chirocentrus dorab (Forssk.)	Richardson, 1846 (Canton*); Fowler, 1930, 1931, (Hong Kong).
Dussumieriidae	
Etrumeus teres (DeKay)	Whitehead, 1963*b*, p. 374 (Hong Kong); Hong Kong*
Dussumieria acuta Valenc.	Herre & Myers, 1931 (Hong Kong); Hong Kong.*
Spratelloides gracilis (Schlegel)	[Whitehead, 1963*a*, p. 375—Formosa*; Fowler, 1941—Philippines]; Hong Kong.*
Clupeidae	
(Clupeinae)	
Sardinella aurita Valenc.	Richardson, 1846 (on Reeves illustr. of *C. nymphaea*); [Kishinouye, 1907—Amoy, Swatow; Chan, 1965—Taiwan]; China*.
†*Sardinella brachysoma* Blkr.	[Chu & Tsai, 1958—Formosa, as *S. albella* (Val.).]
†*Sardinella bulan* (Bleeker)	[Bleeker, 1873—Amoy]; Amoy*.
Sardinella jussieu (Lac.)	Fowler, 1931 (Hong Kong); Amoy*, Hong Kong*.
Sardinella fimbriata (Valenc.)	Richardson, 1846—as *C. isingleena;* Hong Kong*.
Sardinella leiogaster Valenc.	Kner, 1865 (Hong Kong); Richardson, 1846—as *C. caeruleo-vittata;* ? Jouan, 1867—Hong Kong, as *Harengula moluccensis.*
†*Sardinella clupeoides* (Blkr.)	[Kishinouye, 1907—Japan, as *C. okinawensis;* Fowler, 1941—Philippines; Chan, 1965—Thailand, Philippines].
†*Herklotsichthys schrammi* (Bleeker)	[Chu & Tsai, 1958—Formosa].
†*Herklotsichthys punctatus* (Rüppell)	[Chu & Tsai, 1958—Formosa]; Philippines*.
†*Herklotsichthys zunasi* (Bleeker)	[Fowler, 1951—Japan, Philippines]; Japan*, East Indies*.
(Alosinae)	
Hilsa (*Tenualosa*) *reevesii* (Rich.)	Richardson, 1846; Whitehead, 1965*a* (Hong Kong*).
Hilsa (*Tenualosa*) *toli* (Valenc.)	Fowler, 1931 (Hong Kong, as *Macrura sinensis*); [Jordan & Evermann, 1902—Formosa].
(Pristigasterinae)	
†*Pellona ditchela* Valenc.	[Liu & Shen, 1957—Taiwan, as *Ilisha hoeveni*].

* Specimen in British Museum from this locality. [ ] references from other areas.

† Species may occur in Hong Kong waters, but no record or specimen.

Ilisha elongata (Bennett)	Richardson, 1846 (China Seas*); Valenciennes, 1847 (Macao); Kner, 1865 (Hong Kong); Fowler, 1931 (Hong Kong); Chen, 1961 (Quemoy); Amoy*.
Ilisha brachysoma (Bleeker)	Fowler, 1931 (Hong Kong); Hong Kong*.
Ilisha indica (Swainson)	Norman, 1923 (Hong Kong*); [Chen, 1961—Quemoy].
Ilisha novacula (Valenc.)	Norman, 1923 (China*).
Opisthopterus tardoore (Cuvier)	Fowler, 1931 (Hong Kong).
Opisthopterus valenciennesi Blkr.	Foochow*, Hong Kong*.
(Dorosomatinae)	
Konosirus punctatus (Schlegel)	Richardson, 1846 (Chinese sea*); Herre & Myers, 1931 (Hong Kong); Amoy*.
Clupanodon thrissa (Linn.)	Osbeck, 1757 (Canton); Richardson, 1846 (on Reeves illustr. and specimen from Canton*); Fowler, 1930, 1931 (Hong Kong); Herre, 1934 (Hong Kong); [Liu & Shen, 1957—Taiwan].
Nematalosa nasus (Bloch)	? Richardson, 1846 (on Reeves illustr.); Jordan & Seale, 1905 (Hong Kong); Herre, 1934 (Hong Kong); Hong Kong*.
Nematalosa japonica Regan	Herre & Myers, 1931 (Hong Kong); Hong Kong*.
†*Anodontostoma chacunda* (Ham. Buch.)	[Fowler, 1941—Hainan, Philippines].
ENGRAULIDAE	
Engraulis japonicus (Schlegel)	Chefoo*, Hong Kong* [Whitehead, 1964—Japan*, East Indies].
Stolephorus commersonii Lac.	Richardson, 1846 (China*); Fowler, 1930 (Hong Kong); Hong Kong*.
Stolephorus indicus (van Hass.)	Seale, 1914 (Hong Kong); Herre & Myers, 1931 (Hong Kong); [Chen, 1961—Quemoy]; Hong Kong specimens, Zool. Mus. Copenhagen.
Stolephorus buccaneeri Strasburg	Formosa*; [? Chen, 1961, as *S. zollingeri*—Quemoy]; Hong Kong*.
Stolephorus tri (Bleeker)	[Bleeker, 1865—Amoy;]Liu & Shen, 1957—Taiwan]; Hong Kong*.
Stolephorus heterolobus (Rüpp.)	Hong Kong*; [Liu & Shen, 1957—Taiwan, as *S. pseudoheterolobus*].
Thryssa mystax (Schneider)	Osbeck, 1757 (Canton); Richardson 1844–5, 1846 (China Seas); Jordan & Seale, 1926 (Hong Kong); Herre & Myers, 1931 (Hong Kong); Herre 1934 (Hong Kong).
†*Thryssa setirostris* (Brouss.)	[Fowler, 1941—Philippines]; Amoy*.
Thryssa dussumieri (Valenc.)	Seale, 1914 (Hong Kong); [Chen, 1961—Quemoy].
†*Thryssa hamiltonii* (Gray)	[Mori, 1952—Japan; Fowler, 1931—Philippines]; China*.
Setipinna taty (Valenc.)	Fowler, 1931 (Hong Kong).
Coilia mystus (Linn.)	Osbeck, 1757 (Canton); Richardson, 1844–5, 1846 (China Seas*); Jordan & Seale, 1926 (Hong Kong).
Coilia playfairii (McClelland)	Richardson, 1845 (Hong Kong); Kner, 1865 (Hong Kong); Fowler, 1930, 1931 (Hong Kong); Nichols, 1943 (Anhwei, nr. Canton); China*.

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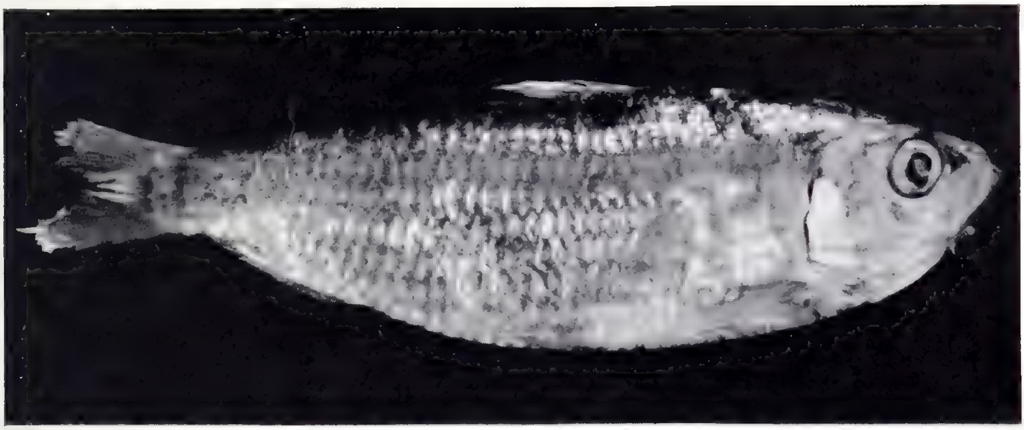
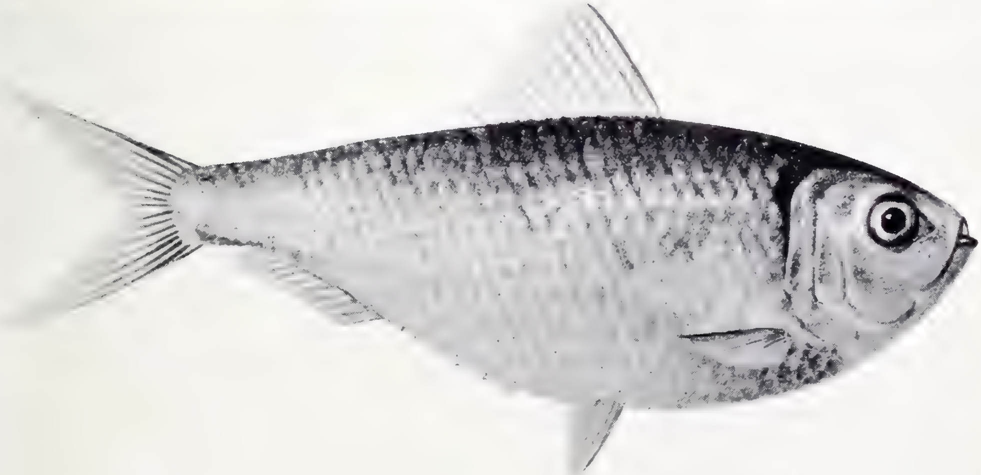
PLATE 1

FIG. 1. *Clupea isingleena* Richardson, holotype (108·5 mm. S.L., BMNH. 1963. 6.17.1). Formerly believed holotype of *C. nymphaea,* see text, p. 24.

FIG. 2. *Clupea isingleena,* Reeves drawing No. 60 [= *Sardinella fimbriata* (Val.)].

FIG. 3. *Clupea nymphaea,* Reeves drawing No. β25 [= *Sardinella aurita* Val.].





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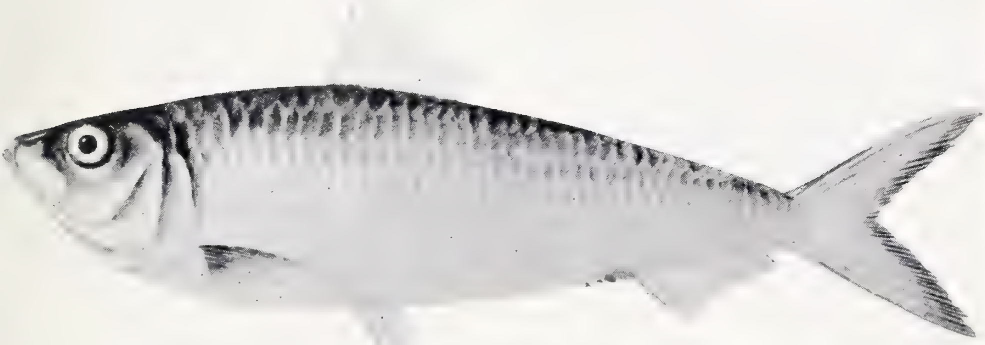

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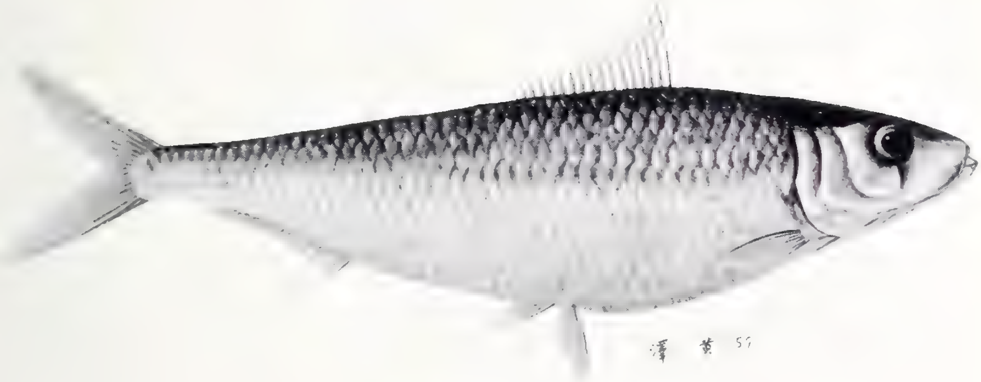
PLATE 2

FIG. 1. *Clupea caeruleo-vittata*, Reeves drawing No. 59 [= *Sardinella*, probably *S. leiogaster* Val.].

FIG. 2. *Clupea flosmaris*, Reeves drawing No. 64 [= *Herklotsichthys* or *Sardinella* sp.].

FIG. 3. *Alosa reevesii*, Reeves drawing No. *a*8 [= *Hilsa reevesii* (Rich.)].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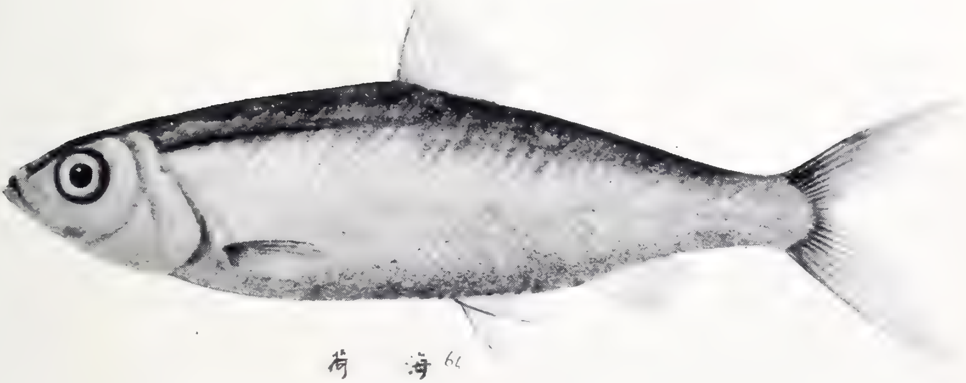
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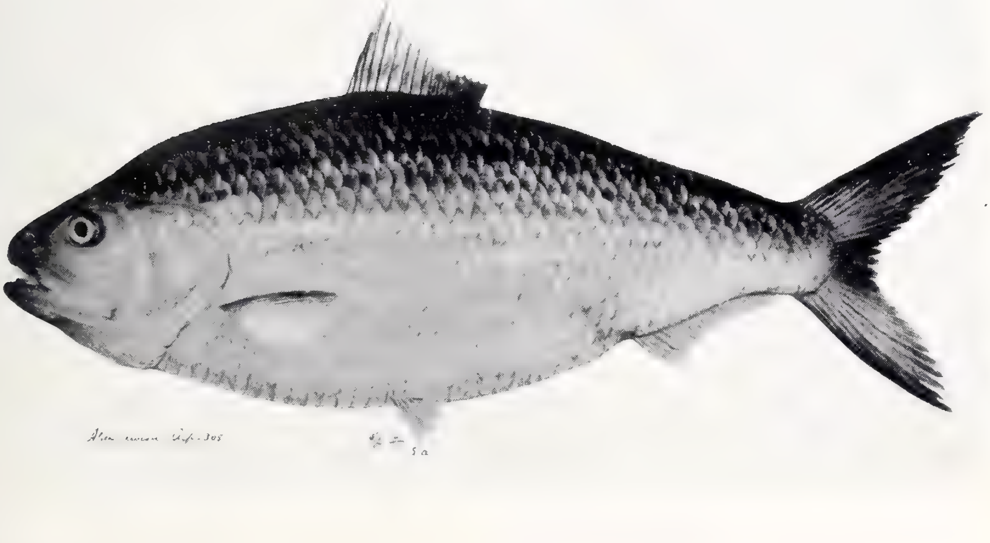
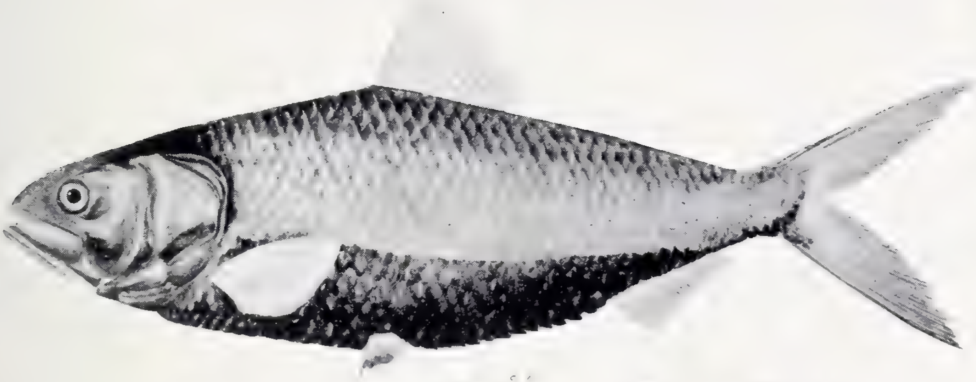

Alosa [illegible] Inf. 305
5a

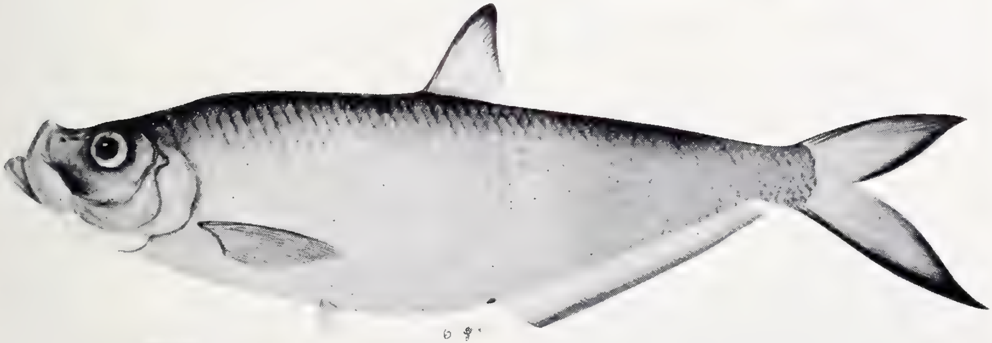
PLATE 3

FIG. 1. *Alosa palasah,* Reeves drawing No. β51 [= *Hilsa reevesii* (Rich.)].

FIG. 2. *Ilisha abnormis,* Reeves drawing No. 81 [= *Ilisha elongata* (Bennett)].

FIG. 3. *Ilisha abnormis,* Reeves drawing No. 67 [= *Ilisha elongata* (Bennett)].





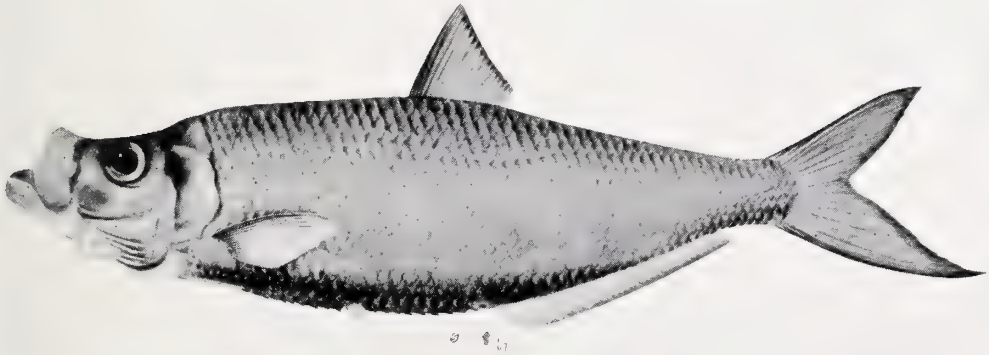


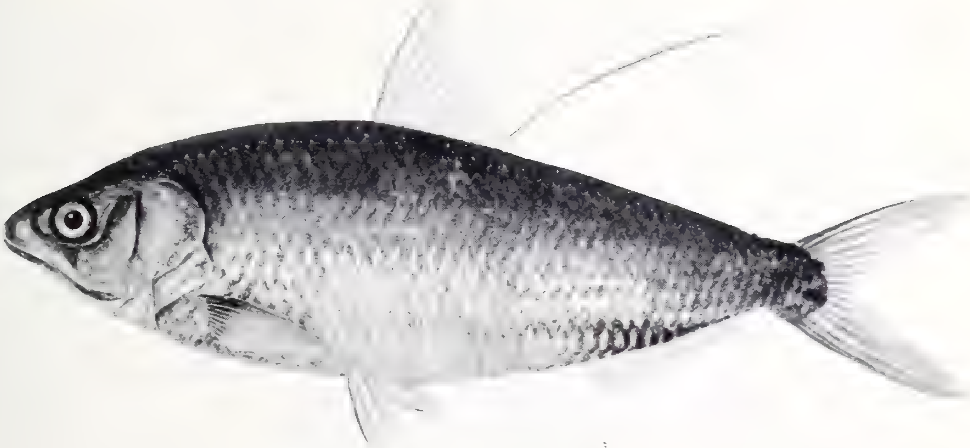
PLATE 4

Fig. 1. *Chatoessus aquosus,* Reeves drawing No. 63 [= *Konosirus punctatus* (Schl.)].

Fig. 2. *Chatoessus triza,* Reeves drawing No. 224 [= *Clupanodon thrissa* (L.)].

Fig. 3. *Chatoessus chrysopterus,* Reeves drawing No. 61 [= *Nematalosa,* probably *N. nasus* (Bloch)].

PLATE 4



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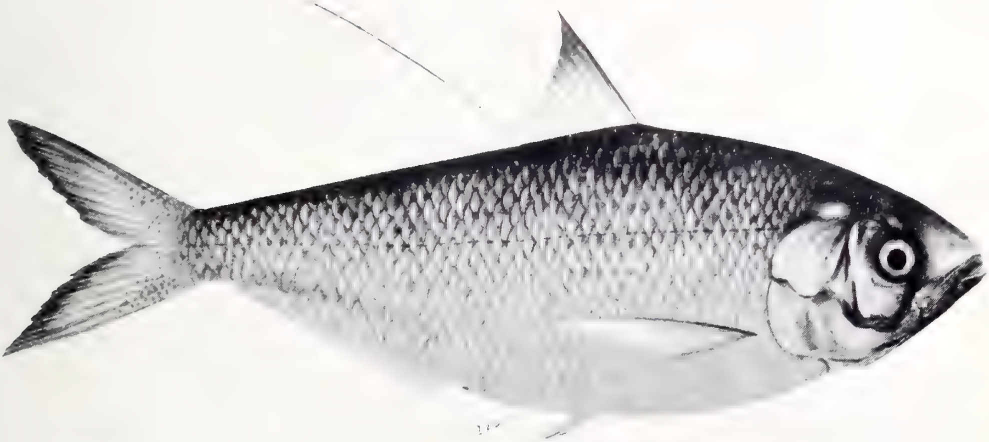

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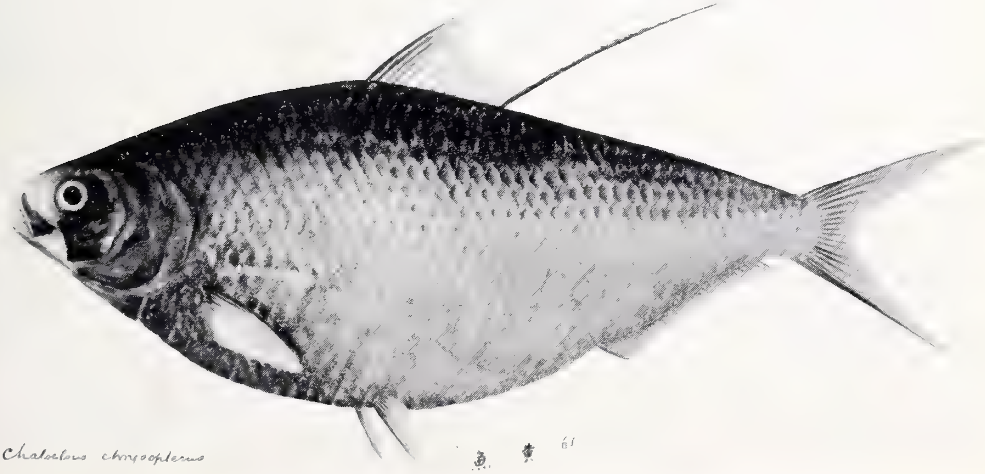


Chalcelus chrysopterus

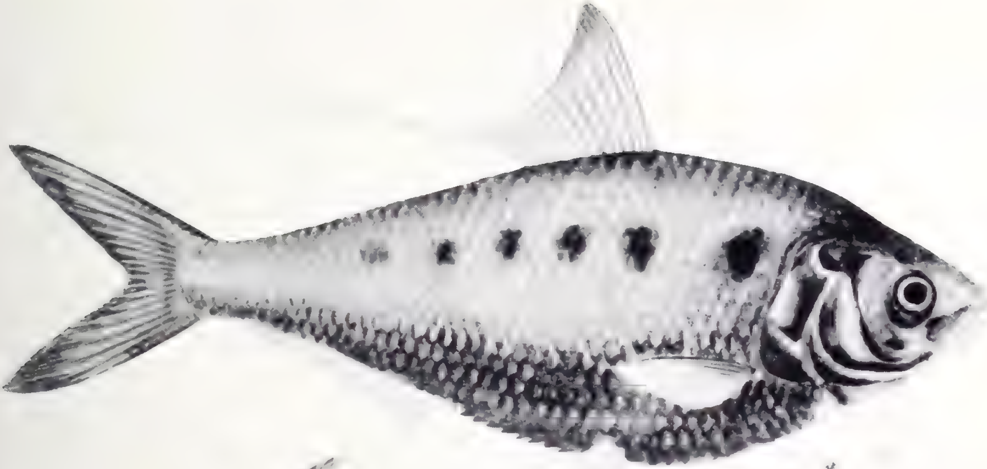
黄魚 61

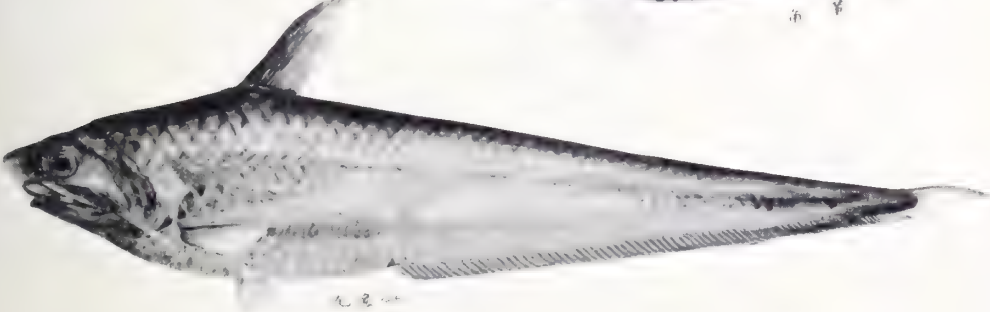
PLATE 5

FIG. 1. *Chatoessus maculatus,* Reeves drawing No. 109 [= *Clupanodon thrissa* (L.)]

FIG. 2. *Coilia grayii,* Reeves drawing No. α14 [= *Coilia mystus* (L.)].

FIG. 3. *Coilia playfairii,* Reeves drawing No. β26 [= *Coilia playfairii* (McClelland)].





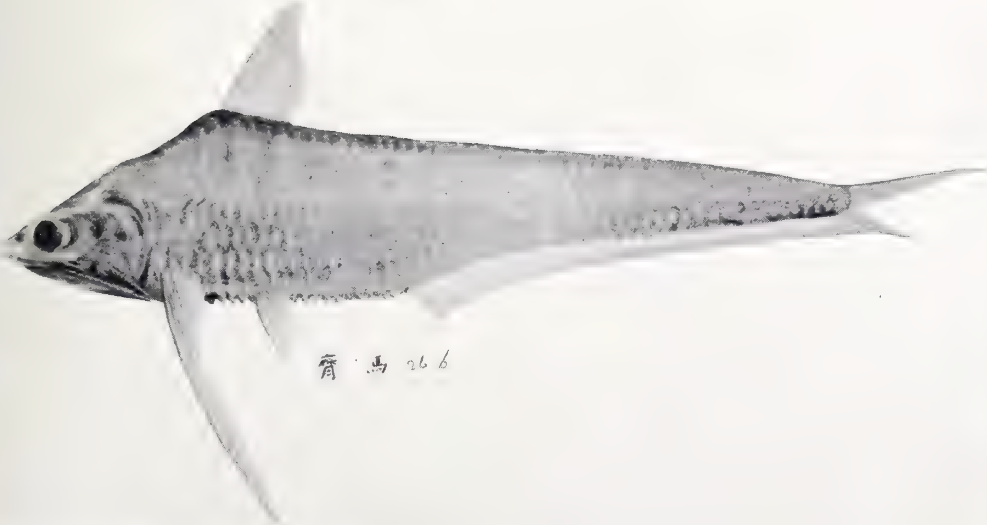
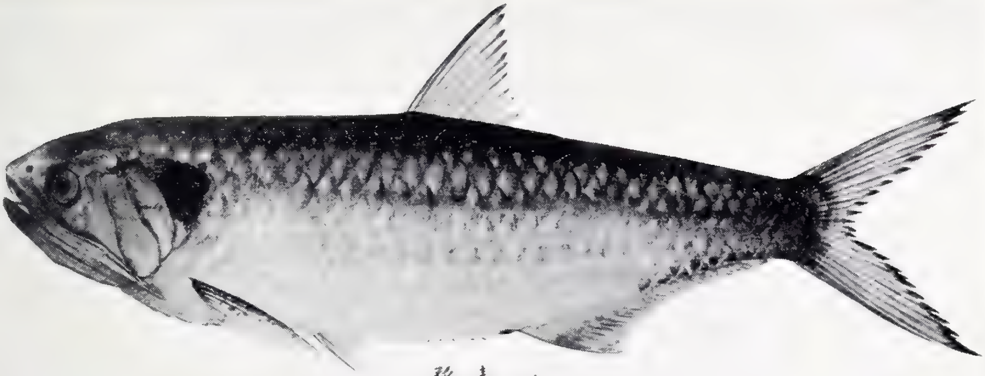

齊 馬 26 b

PLATE 6

FIG. 1. *Thryssa mystax,* Reeves drawing No. 138 [= *Thryssa mystax* (Schneider)].

FIG. 2. *Megalops setipinnis,* Reeves drawing No. 96 [= *Megalops cyprinoides* (Broussonet)].

FIG. 3. *Megalops curtifilis,* Reeves drawing No. 136 [= *Megalops cyprinoides* (Broussonet)].



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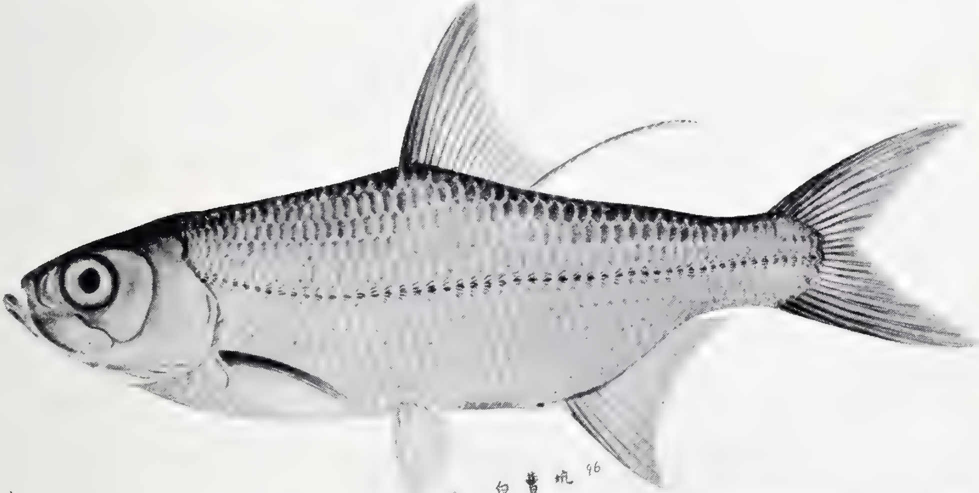

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Megalops setipinnis Rich 610

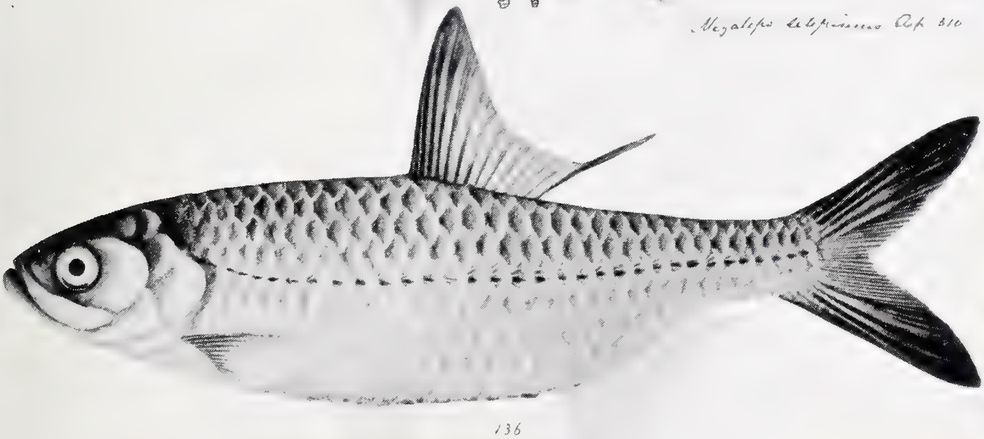

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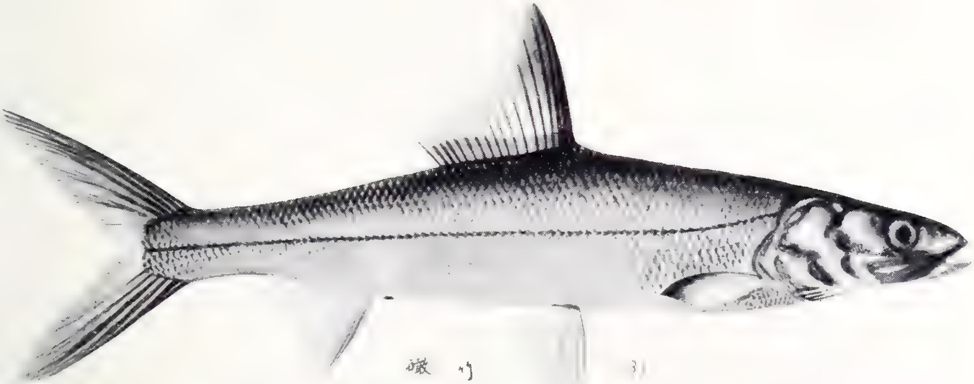
PLATE 7

FIG. 1. *Elops machnata*, Reeves drawing No. 137 [= *Elops machnata* (Forsskål)].

FIG. 2. *Elops purpurescens*, Reeves drawing No. 53 [= *Elops machnata* (Forsskål)].

FIG. 3. *Chirocentrus dorab*, Reeves drawing No. 47 [= *Chirocentrus dorab* (Forsskål)].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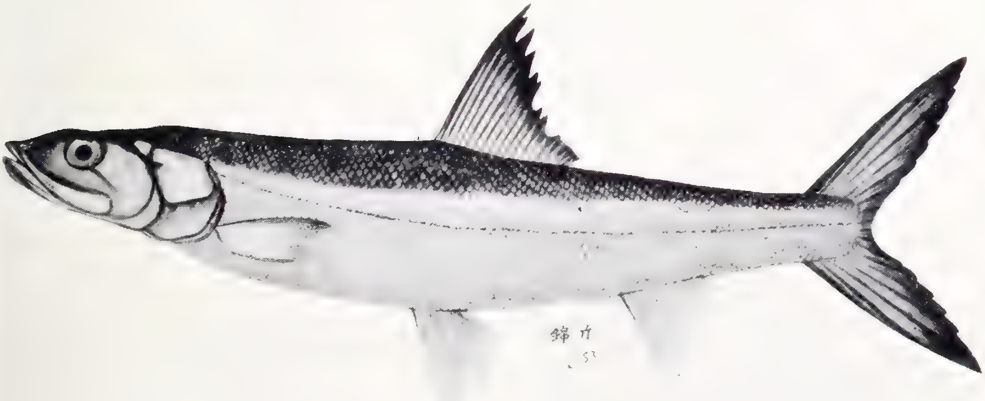
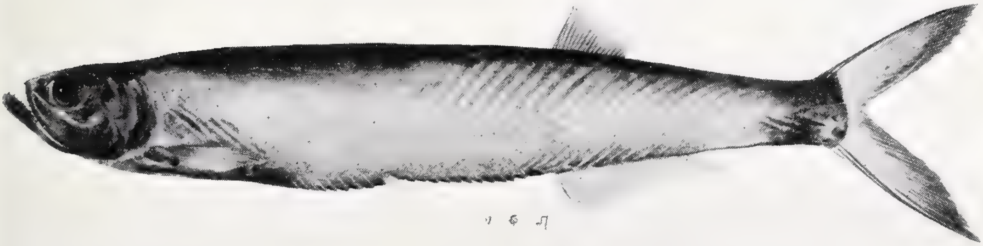

52
Elops purpurascens. Cop. p.


Chirocentrus dorab. Cuv. p. 311.

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OBSERVATIONS ON THE TYPE-MATERIAL OF SOME GENERA AND SPECIES OF POLYZOA

ANNA B. HASTINGS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 14 No. 3
LONDON: 1966

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TRING

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BY

ANNA B. HASTINGS

Pp. 55–78 ; 1 *Plate* ; 1 *Text-figure*

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By ANNA B. HASTINGS[1]

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1. INTRODUCTION

In this paper I have gathered together the results of the examination of the type-specimens of a number of species.

2. CHALLENGER COLLECTION

The two main sets of Challenger Polyzoa (received by the Museum in 1887 and 1899, see Hastings, 1943 : 304) have been supplemented by further material from the Busk Collection, received in 1943 (registration 1944.1.8.1–406), among which some figured, and otherwise informative, specimens have been found. There is also a series of preparations of chitinous parts, made by Busk from Challenger specimens, received by the Museum in 1882. All these collections include syntypes of Busk's Challenger species.

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[1] Address: 28, Kew Gardens Road, Richmond, Surrey, England.

3. SOME TYPE-SPECIMENS

It has seemed best to arrange these notes, on the examination of sundry type-specimens, alphabetically according to the names under which the species were originally described. An indication of the present generic attribution of each species is given.

Bifaxaria corrugata Busk and ***B. papillata*** Busk

(Text-fig. 1A, B, C)

HARMER'S ELUCIDATION OF THE CHALLENGER REPORT. Harmer (1957 : 868) elucidated Busk's confusion between *Bifaxaria corrugata* and *B. papillata*, both of which (pp. 867, 868) he referred to *Sclerodomus* Levinsen. Harmer did not see Busk's drawings (published or unpublished), nor his copy of the Challenger Report. They have yielded evidence, in Busk's hand-writing, confirming Harmer's conclusions. The details are filed in the British Museum (Nat. Hist.).

Harmer's conclusions may be summarized thus: Busk's pl. XIII, figs. 4, 4a, described as *B. papillata*, represent *B. corrugata*[1]; and his pl. XXIV, fig. 6, described as *B. corrugata*, represents *B. papillata*; the attributions of pl. XIII, figs. 3, 3a to *B. corrugata* and pl. XXIV, figs. 4 A–D to *B. papillata* are correct. *B. corrugata* was obtained solely at St. 122, and *B. papillata* solely at St. 196.

With only four exceptions (pl. XIII, fig. 4, one zoarium, and pl. XXIV, figs. 4B, 4C and 6, see below) all the figured specimens are definitely recognizable by their detailed agreement with the figures. Harmer's identification of these specimens agrees with Busk's original labelling. In the subsequent confusion Busk altered the name on one slide (1887.12.9.379A changed from *B. corrugata* to *B. papillata*, presumably because the specimen is shown in pl. XIII, fig. 4, left hand figure, under that name). Kirkpatrick (MS. Catalogue) accepted this, and added a label to the slide. These are the alterations mentioned by Harmer.

To sum up, the specimens are mounted on three slides, and are figured as follows:

1887.12.9.377, *B. corrugata*, St. 122.

Left hand zoarium is represented in pl. XIII, fig. 3 (nat. size), and fig. 4a.

Right hand zoarium is represented in pl. XIII, fig. 4, right-hand figure (nat. size).[2]

1887.12.9.379A, *B. corrugata*, St. 122, is represented in pl. XIII, fig. 4, left-hand figure (nat. size), and fig. 3a.

---

[1] He should have excluded one of the three zoaria in fig. 4 from *B. corrugata* (see below).

[2] It will be noticed that the figures of the zoaria are mostly placed with magnified figures of the same species, but not always with those of the same specimen. The original drawings of the zoaria were (with one exception) not on the same cards as the magnified drawings, which perhaps led to the errors in arranging them on the plate. None of the original drawings of zoaria have been preserved; even the one on the same card as other drawings was cut out, and a note made beside the hole.

1887.12.9.379, *B. papillata*, St. 196, is represented in pl. XXIV, figs. 4A and 4D. Figs. 4B, 4C and 6 (pl. XXIV) show no peculiarities by which the figured zooecia can be recognized, but they closely agree with the zooecia of comparable age in this specimen.

The pieces mounted on this slide (1887.12.9.379) are evidently parts of one colony, which appears to have been the central zoarium of three figured in pl. XIII, fig. 4; but I have not proof of this. The presence of secondary branches does, however, support the conclusion that this drawing represents *B. papillata* (see footnote 1 on p. 58).

LECTOTYPES:

a. *B. corrugata*. Harmer's choice (1957 : 868) of the specimen 1887.12.9.379A as " type ", in his list of specimens, and " type-specimen " in the text, constitutes a valid choice of lectotype.

b. *B. papillata*. I have said above that the fragments on the slide 1887.12.9.379 are evidently parts of one colony. If this could be proved the whole slide would be holotype by monotypy. In the absence of proof, I have chosen as lectotype the lower (larger) of the two pieces figured in pl. XXIV, fig. 4A.

SYSTEMATIC POSITION. The frontal wall of *Sclerodomus corrugatus* and *S. papillatus* is arched over a frontal membrane with a membraniporine operculum. The wall is thus of the nature of a frontal shield, and these species belong to the Ascophora imperfecta of Harmer (1957 : 645, 651).

I am not confident that Harmer was right in referring these two species to *Sclerodomus*, the type-species of which, *S. denticulatus* (Busk), was well described by Levinsen (1909 : 302). Levinsen (p. 304) examined a small fragment of Busk's material of *Bifaxaria corrugata* and had " no doubt that this species belongs not only to another genus but even to another family than *Sclerodomus denticulatus* ". I have not seen Levinsen's fragment, but it evidently came from an old part of the zoarium and may in some ways have misled Levinsen, as also did Waters's description of the ovicell (1888 : 15)—" formed by a swelling of the superjacent zooecia ". Both species have normal ovicells (cf. Harmer, 1957 : 869). Nevertheless, there are differences (e.g. the absence of an avicularian cross-bar, which is sometimes thought to be important).

COMPARISON OF THE SPECIES. *S. papillatus* and *S. corrugatus* differ markedly in the details of their primary frontal walls (Text-fig. 1A, C). In both there is a median longitudinal line (" keel ") which is a little more thickly calcified (cf. Harmer, 1957 : 866). In *S. papillatus* this line runs up into a prominent, mucro-like lip (Text-fig. 1C), except in fertile zooecia where the edge of the frontal shield is transverse (Harmer, pl. LVII, fig. 16 as *S. corrugatus*, see below). In *S. corrugatus* the longitudinal line is less pronounced. The edge of the shield is more or less transverse (Text-fig. 1A), or slightly prominent, in the non-fertile zooecia, and in the fertile zooecia it forms a broad rounded lip (Busk, pl. XIII, fig. 3a). In *S. papillatus* the pores are peripheral, arranged in one or two series. Sutures or cracks run outward from the median line, most of them ending in a pore. In *S. corrugatus* the pores are central, arranged on each side of the median line in several longitudinal series, and there are no sutures or cracks. Laterally there are longitudinal ridges, and the extension and thickening of this ridged calcification forms the striated thickening which gradually obliterates the original frontal wall and transforms the appearance of the older parts of the colony by enveloping the branches. The pores are continued upwards as oblique tubes in this thickening, the oblique transection of the tubes and the wall giving the appearance of oval or elongate pores (Text-fig. 1A). In *S. papillatus* it is the develop-

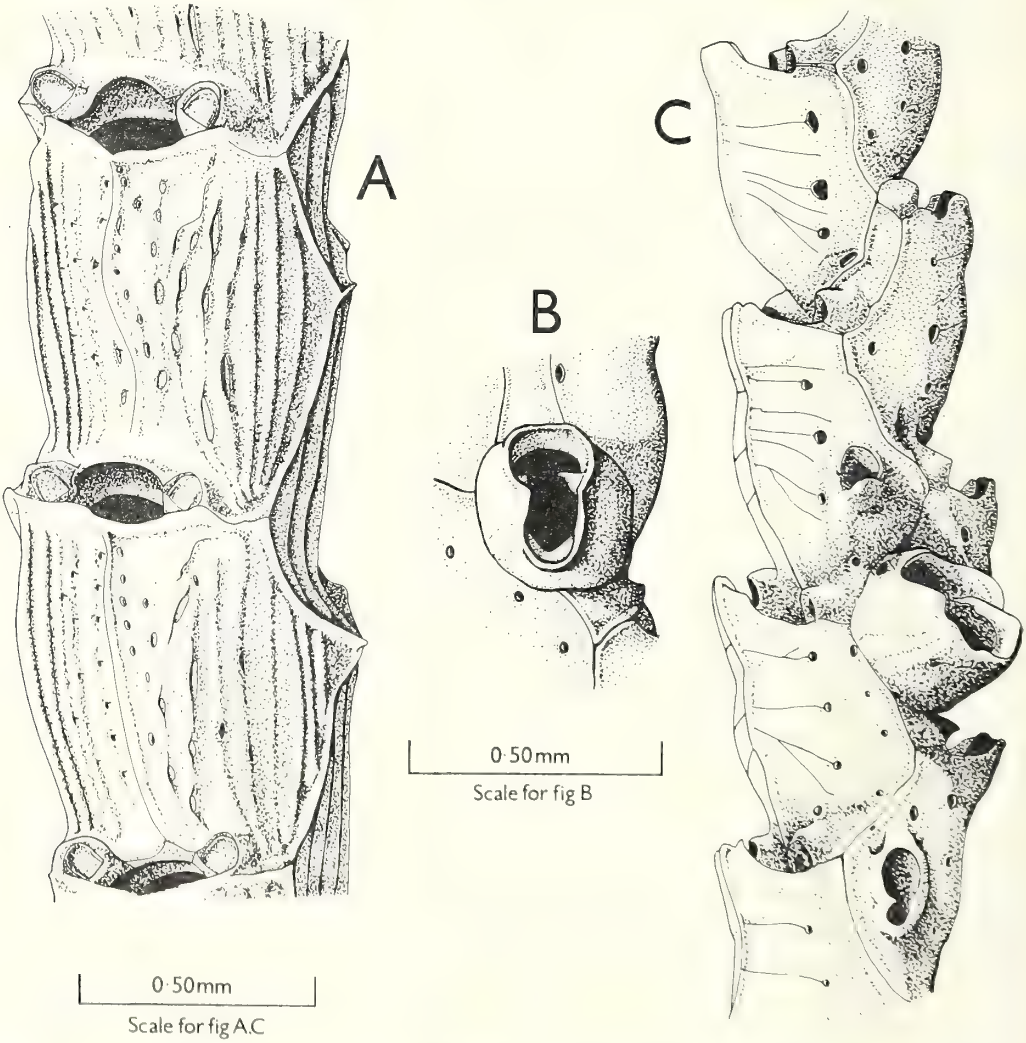

Fig. 1. *Sclerodomus corrugatus* and *S. papillatus*. Zooecia near the growing point for comparison of their characters before obliteration of the primary walls by secondary developments. A. *S. corrugatus*, 1887.12.9.379A, lectotype. B, C. *S. papillatus*, 1964.2.2.4, Siboga collection, specimen 583A^1. B. is the large avicularium which is seen obliquely in C.

ment of a covering of avicularia which leads to marked differences in the appearance of the branches at different stages. The youngest branches are slender with almost hyaline, glistening zooecia, in which the lateral frontal-pores and the fine sutures can quite readily be seen. As they get older they become opaque, and the covering of avicularia begins to develop down each side of the branch. The oldest branches are covered with a mosaic of these avicularia, which makes them considerably thicker than the younger branches ; and a large avicularium is frequently developed at the bifurcations (but not in the axils). The first avicularia to appear are single lateral ones on each side of each zooecium, forming a zig-zag series down each side of the branch. An occasional one of these is enlarged. In fig. 1C the first lateral avicularia have appeared, the youngest zooecia still being without them. One is large (figs. 1B and C) and the most proximal is not fully developed.

Identity of the Siboga material. The difference in age of the specimens probably accounts for the rather surprising fact that, having correctly elucidated Busk's work on these two species, Harmer (1957, p. 869) was in doubt as to the identity of the Siboga species, and finally placed it in *S. corrugatus*. The Siboga specimens agree perfectly with *S. papillatus*, and differ from *S. corrugatus*, in the shape of the zooecia and peristome, the distribution of the pores, the presence of a lateral avicularium on each zooecium and of enlarged ones beside some of the ovicells, the presence of secondary branches, and the covering of the older parts by avicularia. This covering was not described by Busk, but its earlier stages are present on the proximal part of the main axis of the Challenger specimen of *S. papillatus*. Busk's pl. XXIV, fig. D resembles Harmer's pl. LVII, fig. 10 with remarkable closeness. Only the large lateral avicularium is absent in the Siboga figure, but these are present in the Siboga material.

The apparent differences between the Siboga material and the type-specimen of *S. papillatus* lie wholly in their age. The type-specimen consists almost entirely of branches in the younger phases, the most proximal having reached the phase with a zig-zag line of avicularia, and no older phases being represented. The greater part of the Siboga material is in the oldest phase, and there are only few young branches. It therefore looks decidedly stouter than the type-specimen, and different in surface sculpture, etc. ; but if branches in the same phase are compared the agreement in all characters, including dimensions, is found to be exact[1], except for the absence of enlarged avicularia at the bifurcations in the Challenger specimen. As they only appear in the older, thicker parts of the Siboga material, the difference in the age of the material probably also accounts for this.

Station 122, type-locality of *S. corrugatus*, is off Brazil, and Station 196, type-locality of *S. papillatus*, is off Celebes. Thus the geographical probabilities also support my conclusion that the Siboga material belongs to *S. papillatus*.

The synonymies of the two species given by Harmer (pp. 867, 868) are, as already indicated, correct ; but the one to be applied to the Siboga specimens is that given for *Sclerodomus papillatus* (p. 868).

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[1] Miss Cook (in litt.), " I have made several sets of measurements and the agreement is quite startling. ' Exact ' is certainly the right word ",

Flustra octodon Busk

Flustra octodon Busk, 1852 : 49, pl. LVI, fig. 4, pl. LVIII, fig. 5.
Hincksinoflustra octodon Bobin & Prenant, 1961 : 167 (as *Flustra octodon*), 169, 170, text-fig. 4I–IV.
Hincksina (*Flustra*) *octodon* (Busk) Gautier, 1962 : 51. (*Hincksinoflustra* in text. Synonymy.)

DISTRIBUTION. Coast of Spain (probably Mediterranean) ; Mediterranean ; Atlantic coast of Morocco.

LECTOTYPE, chosen here : 1899.7.1.112B.

PARALECTOTYPES. 1899.7.1.5789. 1963.3.12.1 (previously unregistered).

LOCALITY OF THE TYPE-MATERIAL. This material consists of two spirit specimens, figured by Busk (1852, pl. LVI, fig. 4 ; left-hand figure, 1899.7.1.5789 ; right hand figure, 1899.7.1.112B), a slide from which pl. LVIII, fig. 5 was drawn (1963.3.12.1), and two preparations made in comparatively recent years from 112B. All these specimens came from M'Andrew's Spanish collection, and the locality published by Busk is " Coast of Spain, M'Andrew ".

The question arises as to whether the specimens came from the Atlantic or the Mediterranean side of the peninsula. Busk (1852, 1854) published descriptions of M'Andrew's Polyzoa as follows : from the " Coast of Spain ", *Alysidium lafontii* (p. 14), *Scrupocellaria macandrei* (p. 24) and *Flustra octodon* (p. 49) ; from the " Bay of Gibraltar ", *Membranipora rossellii* (p. 59), *M. calpensis* (p. 60), *Lepralia violacea* (p. 69), *L. spinifera* (p. 70) ; from the " Mediterranean ", *Lepralia linearis* (p. 71), *Eschara foliacea* (p. 89).

The slide of *A. lafontii* (1899.7.1.3752) has labels superimposed on the old ones, as was Busk's custom[1]. The original label reads " Coast of Spain ", the newer one " Mediterranean ". The original drawings of *S. macandrei* (pl. XXIV, fig. 1), and *F. octodon* (pl. LVIII, fig. 5) are both inscribed " Mediterranean ".

Conversely, three of the four slides of the two species recorded as from the Mediterranean, are labelled " Coast of Spain ". The four slides are : *L. linearis*. S. Coast of Spain, 72–128 fms., 1899.7.1.2330 ; Mediterranean, 1899.7.1.2319. *E. foliacea*, Coast of Spain, 1899.7.1.1417 ; S. Coast of Spain, 1899.7.1.1412.

There is thus evidence that suggests that all the M'Andrew Spanish material described by Busk in the British Museum Catalogue came from the Mediterranean side of the peninsula.

The locality given on the specimen of *Flustra octodon*, illustrated in pl. LVI, fig. 4 (right-hand specimen), is " Between Vigo Bay and Tunis ". Unless this is an error, it must be a generalization covering the area visited by M'Andrew, and would not be incompatible with a Mediterranean origin for the specimen.

Flustra octodon is the type-species of *Hincksinoflustra* Bobin & Prenant (1961).

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[1] His specimens were relabelled, sometimes more than once, in accordance with changes in the style of label in use in his collection ; for further details see Hastings, MS. note in Busk Register, British Museum (Natural History).

Lepralia melolontha Landsborough

Lepralia nitida, branched in a fine dendritic manner, Johnston, 1847 : 319.
Lepralia nitida, specimen *d.*, " *Lep. nitida* var.", Gray, 1848 : 121.
Lepralia melolontha Busk; Landsborough, 1852 : 319, pl. XVIII, fig. 70; Busk, 1854 : 79, pl. LXXXV, fig. 3.
Membraniporella melolontha Busk Hincks, 1880*a* : 202, pl. XXVII, figs. 9, 10.
Aspidelectra melolontha Levinsen, 1909 : 160.
Aspidelectra melolontha Busk : Marcus, 1940 : 199, text-fig. 103.

DISTRIBUTION. This species is only known from localities of more or less reduced salinity bordering the North Sea. The distribution given by Marcus is Denmark (one locality, Horns Rev[1]); Heligoland; Belgium; southern England [eastern England would be more correct].

LECTOTYPE, chosen here: 1854.11.15.140, British Museum Catalogue Coll. Thames Estuary, Lieut. Thomas.

PARALECTOTYPES. 1899.7.1.1363, Busk Coll. Thames Estuary, Lieut. Thomas. 1899.7.1.1364, Busk Coll. Thames Estuary.

OTHER MATERIAL. River Roach, Essex (Dr. Baird, 1865.6.28.1); River Roach (Norman Coll., 1911.10.1.741 part, 1919.6.24.25, 25a, 26); Goodwin Sands, Kent (G. Merritt, 1884.5.10.1); Kirkwall, Orkney (Johnston Coll., Gray 121d, 1847.9.16.130); Locality ? (Hincks Coll., 1899.5.1.727.)

REMARKS. The first published account of this species is by Landsborough. He gave credit to Busk for the discovery of the species, and published a description and drawings supplied by Mrs. Gatty, who had recognized it independently (see Busk). Busk has hitherto been named as the authority for the species, but strictly Landsborough's name should be given. Under these slightly confused circumstances it seems desirable to choose a lectotype.

The Busk material in the Museum consists of three slides from the Thames Estuary material mentioned by Landsborough. These are syntypes, and, in the absence of any of the material figured by Mrs. Gatty, I have chosen one of them as lectotype. The material from Bawdsey, figured by Busk (1854), is not in the Museum, but would not be a syntype.

Hincks (p. 203, footnote) thought that Mrs. Gatty (in Landsborough) was right in identifying Johnston's dendritic variety of *Lepralia nitida* from Kirkwall, Orkney Islands, with this species. Marcus (p. 201) noted the Orkney record as being uncertain but not improbable. It is confirmed by Johnston's specimen (1847.9.16.130, Kirkwall). This consists of several small colonies of *L. melolontha* on pieces of *Mytilus* shell. They are growing with *Electra monostachys* (Busk) and *Conopeum reticulum* (Linn.), an association which suggests a brackish-water habitat. The same three species are, for example, found together from the River Roach, Essex (Norman Coll., 1911.10.1.481 and 483), where one shell in particular shows all three intermingled as in the Orkney specimen.

One of the Johnston colonies of *L. melolontha* has its membraniporine ancestrula intact. It has formed a pair of distal zooecia, each of which has budded a further pair. Only the left-hand zooecium of each of these two pairs has budded, and from these buds the two arms of the colony fan out and diverge—see also Hincks (fig. 10) and Marcus (text-fig. 103) which both show fan-shaped branches starting from a single zooecium.

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[1] Horns Rev, a shoal to the west of Jutland.

L. melolontha is the type species, by monotypy, of *Aspidelectra* Levinsen (1909).

Lepralia multidentata Thornely

Lepralia multidentata Thornely, 1905 : 120, pl. [unnumbered], fig. 9.
Hippoporella multidentata (Thornely) Harmer, 1957 : 1099, pl. LXXIII, figs. 9–12.
Lepralia purpurea Thornely, 1905 : 120, pl. [unnumbered], fig. 13.

DISTRIBUTION. Ceylon ; India ; Sulu Archipelago.

LECTOTYPE, of *L. multidentata*, chosen here : 1906.12.3.4. Ceylon.

PARALECTOTYPE, of *L. multidentata* : Cambridge Museum, Feb. 22, 1906.9. Ceylon.

HOLOTYPE, of *L. purpurea*, the only specimen : 1906.12.3.6. Ceylon.

REMARKS. Under this species Harmer listed three specimens from the Thornely Collection in the British Museum. They are the one chosen here as lectotype, and two (not named by Thornely) which he had himself found, accompanying specimens of other species in the Thornely collection.[1] The Cambridge specimen was named by Thornely and is a syntype.

Harmer recognized *Lepralia purpurea* Thornely as a synonym of *L. multidentata*, but did not list the specimen.

Lunulites owenii Gray

Lunulites owenii Gray, 1828 : 8, pl. III, fig. 15.
Cupuladria owenii (Gray) Cook, 1965 : 213, pl. 2, figs. 3A, B, text-fig. 2C. (Synonymy.)

DISTRIBUTION. *Recent*, West Africa. *Pliocene*, South Carolina ; Florida. *Miocene*, North Carolina ; Florida. (Teste Cook).

LECTOTYPE, chosen here : 1899.7.1.4879, W. Africa.

The slide 1899.7.1.4879, which forms part of the Busk Collection, is labelled " B.M.. J. E. Gray ", indicating that Busk received the specimen from the British Museum. It is the only representative of Gray's material of this species now in the Museum and Kirkpatrick (MS. Catalogue) accepted it as the type-specimen. It is the specimen figured by Busk (1854, pl. CXV, fig. 3).

REMARKS. *Cupuladria owenii* is discussed by Cook.

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[1] Their numbers, incorporating numbers in Harmer's lists, are:
1936.12.30.41A with *Cleidochasma protrusum* 1936.12.30.41D. Ceylon. See Harmer, 1957 : 1040.
1936.12.30.117B on *Celleporaria columnaris* 1936.12.30.117A. India. See Harmer, 1957 : 677.

Membranipora amplectens Hincks

Membranipora amplectens Hincks, 1881*a* : 129, pl. III, fig. 7.
Electra amplectens (Hincks sp.) MacGillivray, 1889 : 322, pl. CLXXXVII, figs. 14, 14*a*; Levinsen, 1909 : 66, 146, 147, pl. IX, figs. 1a, b.
Membranipora amplectens sp. n. [*sic*] Hincks, 1892 : 332. (Named as " type of a new genus ". Introduction of *Heterooecium* follows.)
Membranipora amplectens (*Heterooecium*) Hincks : Waters, 1898 : 671.
Heterooecium amplectens Hincks : Harmer, 1902 : 284.

DISTRIBUTION. Australia.

LECTOTYPE, chosen here : 1899.5.1.702, Hincks Coll. W. Australia.

PARALECTOTYPE : 1899.5.1.703, Hincks Coll. W. Australia.

OTHER MATERIAL. Australia (1897.5.1.497, 498, mounted by Jelly) ; Australia (Vine Coll., 1934.10.20.85, 91) ; Port Phillip Heads, Victoria (Bracebridge Wilson Coll., 1888.11.14.117, 283).

All the specimens listed are growing on algae.

REMARKS. *M. amplectens* is the type-species, by original designation, of *Heterooecium* Hincks (1892 : 332).

Membranipora crassimarginata var. ***erecta*** Busk

Membranipora crassimarginata var. *erecta* Busk, 1884 : 63, pl. XIV, fig. 3.
Acanthodesia perfragilis (MacGillivray) Hastings, 1945 : 98. (Synonymy.)

DISTRIBUTION. Australia.

LECTOTYPE, chosen here : 1944.1.8.160. Challenger St. 162, Bass Strait.

PARALECTOTYPES. 1887.12.9.309. Challenger, St. 162, Bass Strait.

The other paratypes are all marked with the dubious locality, St. 151, Heard Island (see below). They are : 1887.12.9.310, 311 ; 1899.7.1.1004, 1005 ; 1944.1.8.161–164.

REMARKS. Harmer (1926 : 224) accepted a specimen from St. 162, Bass Strait, 1887.12.9.309, as the original of Busk's figure (1884, pl. XIV, fig. 3). The actual figured specimen (1944.1.8.160) had not been deposited in the British Museum at that time. It likewise comes from St. 162 and is recognizable by its detailed agreement with the figure. It was found in the supplementary Busk Collection, received by the Museum in 1943 (see section 2, above). It is chosen here as lectotype.

There is evidence (Hastings, paper in preparation) that Busk's record of Australian species (including this one) from Heard Island (Busk, 1884 : X, those species[1] from St. 151 marked D) may have been due to an error in sorting before the collections were sent to specialists. *M. crassimarginata* var. *erecta* is synonymous with *Acanthodesia perfragilis* (MacG.), see Hastings (1945).

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[1] *Salicornaria clavata* to be excepted. The Heard Island species is distinct from the Australian, see below.

Membranipora hexagona Busk

Membranipora hexagona Busk, 1856 : 308, pl. XII, fig. 4 ; Hincks, 1880*a* : 143, pl. 18, fig. 7 (after Busk) ; 1881*a* : 6, pl. IV, fig. 6.

HOLOTYPE, the only specimen : 1899.7.1.1083. Devon, Miss Cutler.

REMARKS. *Membranipora hexagona* has remained an enigma. Hincks (1880*a* : 143), for example, remarked that he knew " nothing of *M. hexagona* but what may be gathered from the brief description and figure in the ' Zoophytology ' ". He reproduced part of Busk's figure. Subsequently (1881*b* : pl. IV, fig. 6) he figured a specimen lent to him (see 1881*a* : 6) by Busk, presumably the holotype.

Examination of the holotype shows that it is not membraniporine, and that Busk based the name on a mutilated specimen of a species with a calcareous frontal-shield. This shield has been completely broken away in most of the zooecia, and even the lateral walls are somewhat abraded, sometimes exposing the cavities of pore-chambers. On a concave part of the substratum, a few zooecia have been less worn. In these the lateral walls stand higher and in two zooecia small parts of the broken frontal-shield project at the margins of the aperture. The floor of a hyperstomial ovicell also remains. The frontal membranes (which were below the frontal shields) have adhered to the floors of the zooecia, and remained intact, and with them the opercula. The opercula are widely open as in Busk's and Hincks's figures. It is thus clear that *M. hexagona* was based on a misconception.

Supposed material of *M. hexagona* has been recorded from various localities :

Busk himself gave *Flustra coriacea* Johnston (not Esper) as a synonym of *M. hexagona*. *F. coriacea* was recorded by Johnston (1847 : 348, pl. LVI, fig. 8) from specimens from Sana Island, Fowey and the Isle of Man. Busk listed all three localities in the distribution of *M. hexagona*, but Hincks considered that only the specimen[1] from the Isle of Man (collected by Forbes, whose description was used by Johnston) should be identified with Busk's species. This was the first supposed record of *M. hexagona* from the Isle of Man. Two subsequent records were included in the first edition of the Fauna List (Moore, 1937 : 199). The specimens are not available and their identity cannot be surmised.

Smitt (1867 : 371) tentatively included *M. hexagona* in the synonymy of *Membranipora pilosa* forma *membranacea* (Müll.). The latter is a synonym of *Electra crustulenta* (Pallas), and Smitt evidently misinterpreted Busk's figure as showing the calcified opercula characteristic of that species.

Calvet (1896 : 253) identified material from 180 m. in the Gulf of Gascony as *M. hexagona*. There is no clue to its true identity.

Cipolla (1921 : 204) recorded Pliocene fossils from Sicily as *Membranipora exagona*

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[1] No other evidence has, however, been produced for thinking that Johnston confused two species under *Flustra coriacea*. It appears that only the Sana Island specimens came to the British Museum in the Johnston Collection, for they alone are listed by Gray (1848 : 115), and no others have been traced in the collection. These specimens belong to *Micropora coriacea* as generally understood, and include the specimen chosen by Brown (1952 : 126) as lectotype of *Flustra coriacea* Johnston not Esper. The existence of a second British species of true *Micropora* (*M. normani* see below) does not affect this question of whether Johnston may have confused a *Membraniporine* species with *M. coriacea*.

[*sic*] and quoted earlier uses of the name by Fischer (1870) and Neviani (1896 and 1900).

Bassindale (1940 : 194) included Busk's original record in his list of Polyzoa of the Severn Estuary. He noted (p. 197) that a later record from that region (Purchon, 1937 : 329 as *M. hexagonia* [*sic*]) was based on specimens of *Alcyonidium polyoum* (Hassall), one of which I have seen.

Cellepora hexagona von Hagenow (1839) was referred to *Membranipora* by Voigt (1959 : 29, see also Berthelsen, 1962 : 51), and thus became a senior homonym of *M. hexagona* Busk.

Membranipora pilosa var. ***multispinata*** Hincks

Membranipora pilosa var. *multispinata* Hincks, 1882 : 117, pl. V, fig. 6.
Membranipora multispinata Hincks, 1892 : 334 ; 1895 : iii footnote ; Waters, 1924 : 607, 608, pl. XIX, fig. 9 (as *multispina* on p. 607, and as *multispinosa* in expl. pl.).

DISTRIBUTION. Western Australia.

LECTOTYPE, chosen here : 1899.5.1.700, Hincks Coll., mounted by Jelly. W. Australia.

OTHER MATERIAL. 1897.5.1.491, specimen figured by Waters ; 1897.5.1.492. Both from W. Australia and mounted by Jelly. There is no evidence as to whether Hincks saw these two specimens which, being closely similar to the lectotype and also mounted by Jelly, may be parts of the original material. Waters's figure of 1897.5.1.491 is not quite accurate as regards the arrangement of the zooecia in the region which appears to be ancestrular.

REMARKS. There is little to add to Hincks's description. The walls are extremely delicate, glistening and transparent. As described by Hincks, there are five long, more or less stout, socketed spines on each zooecium. They are pointed and may be very long and curved. It appears that the opesia does not extend to the distal end of the zooecium and that the paired spines, described by Hincks as " near the bottom ", are in fact in the distal corners. In addition there may be one to three small, almost thread-like spines, similarly socketed, on the lateral gymnocyst alongside, but at a distance from, the opesia.

The proximal gymnocyst may have a few bright spots, either scattered or arranged in one or two transverse rows near the proximal end. These are the bases of tiny, sharp, thorn-like spines projecting from the inner surface of the transparent wall.

Waters considered that the " articulated " spines distinguished this species from *Electra* and related it to the " *M. corbula* group ". He probably had particularly in mind the series of incurved marginal spines which differ, as he said, from those of *E. pilosa*. The erect spines seem to be remarkably like those seen in some forms of *E. pilosa* and *E. verticillata*, and both the erect and the incurved spines resemble those of *E. monostachys* (Busk), see for example the figure given by Marcus (1950 : 8, text-fig. 1, as *Membranipora* (*E.*) *hastingsae*[1]). *E. multispinata* differs from *E.*

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[1] Examination of type-material has shown that *E. monostachys* is a senior synonym of *E. hastingsae* (Marcus), not a junior synonym of *E. crustulenta* as supposed by Marcus (1950).

monostachys in its additional gymnocystal spines, its internal spinules, its dimensions, fragile texture and transparency ; but to me they seem clearly to be congeneric.

Membraniporella agassizii Smitt

Membraniporella agassizii Smitt, 1873 : 11, pl. V, figs. 103–106 ; Levinsen, 1909 : 17 ; Hastings, 1964 : 258, 262.

HOLOTYPE, the only specimen : Riksmuseum, Stockholm, 262. Off Cojima, Cuba, 450 fms., March 1869, Pourtalès.

This is recognizably the zoarium figured by Smitt.

REMARKS. Each kenozooecium has a small round opesia, closed by a membrane, as shown in Smitt's figure.

At two points an autozooecium has been budded in the kenozooecial crust. In one instance it lies in a plane parallel to the surface of the branch and forms part of the crust. The other one projects at right angles to the parent branch, and, together with some kenozooecia, appears to form the base of an incipient branch.

The changes with age in the zoaria of Polyzoa, particularly in the erect zoaria of some Ascophora, are well-known and may be very marked. Some striking examples in Cretaceous species have been discussed by Voigt (1960) and Wiesemann (1963). In *Membraniporella agassizii* the secondary layer is built up of both kenozooecia and avicularia. In *Sclerodomus papillatus* (see above under *Bifaxaria*) it is mostly, perhaps entirely, made up of a profusion of avicularia. In *Sclerodomus corrugatus* (above) and *Foveolaria elliptica* Busk (Hastings MS.) the original surface is obliterated by massive calcification, with characteristic texture—striated in the one species, perhaps best described as " fibrous-looking " in the other.

No other generic placing has been proposed for *M. agassizii*. The zooecial characters are those of *Membraniporella* and the taxonomic significance of the multiplication of avicularia and kenozooecia is still unknown (cf. Hastings, 1964 : 258).

Menipea fuegensis Busk

Menipea fuegensis Busk, 1852 : 21, pl. XIX, figs. 1–3.

Menipea patagonica Busk (part), 1852 : pl. XXIII, fig. 1 (not p. 22, pl. XXV, figs. 1–3, pl. XXVII, figs. 1, 2).

Tricellaria aculeata (d'Orbigny) ; Hastings 1943 : 356. (Synonymy and distribution.)

DISTRIBUTION. Widely distributed in sub-Antarctic waters.

LECTOTYPE, chosen here : 1854.11.15.262. Falkland Islands. H. [Hooker].

REMARKS. Busk recorded this species from Tierra del Fuego (Darwin) and the Falkland Islands (Hooker), but the only type-material in the British Museum is the one specimen now chosen as lectotype. This specimen was mounted and labelled by Busk as *Menipea fuegensis*, and sent to the Museum as part of the " British Museum Catalogue Collection ", for which see Hastings (1943 : 304). As noted by Hastings (1943 : 359) the ancestrula and first few zooecia of the type were figured by Busk (pl. XXIII, fig. 1), but, by some curious error, under the name *Menipea patagonica.* There is no evidence as to the locality of the material figured in pl. XIX.

Menipea fuegensis Busk is a junior synonym of *Tricellaria aculeata* (d'Orb.).

Micropora normani Levinsen

Micropora sp. Levinsen, 1902 : 7 (footnote).
Micropora normani Levinsen, 1909 : 162, pl. VIII, figs. 3a, 3b (*M. coriacea* on plate, *M. normani* in explanation of plate).
Micropora coriacea Hincks (part) 1880*a* : 174 (specimens with avicularia).

DISTRIBUTION. Southern and western coasts of Great Britain and Ireland from Hastings to Shetland ; west coast of Spain.

NEOTYPE, chosen here : 1911.10.1.623, Norman Coll. Antrim.

Levinsen stated that he had only seen " a little fragment " of this species, and had lost it. A neotype is therefore needed. The specimen chosen was labelled by Norman as " *Micropora* n sp [*sic*] with avicularia, see Levinsen ". It clearly shows the characters of Levinsen's species, including those of the ovicell.

OTHER MATERIAL. Hastings, Sussex, type-locality (1897.5.1.597 mounted by Jelly) ; Antrim, neotype-locality (Hincks Coll., 1899.5.1.737, slide bearing three specimens of *Micropora,* of which two (on shell) are *M. normani* ; Norman Coll., 1911.10.1.744) ; Liverpool Bay (Thornely Coll., 1936.12.30.349 B) ; Guernsey (Norman Coll., 1965.1.2.1 and 1919.6.25.82) ; West coast of Spain (1872.2.3.146).

REMARKS. In addition to the differences noted by Levinsen (presence of avicularia, the characters of the ovicell, " calcified " opercula) these specimens have smaller zooecia and ovicells than are seen in British specimens of typical *M. coriacea*[1], and the pores in the cryptocyst are few and irregularly scattered. Levinsen's figure shows this latter character. Hincks included specimens with avicularia in *M. coriacea* and, except for its more numerous and evenly distributed pores, his fig. 7 (pl. XXIII) appears to represent *M. normani.* His slide 1899.5.1.737 is evidently one of the comparative mounts that he made of British forms[2] and this supports the conclusion that Hincks's specimens with avicularia represented *M. normani.*

I have not confirmed that the opercula are calcified, but they are whitish and evenly granular, in contrast to the clear, brown, chitinous opercula of *M. coriacea.* The avicularia are sporadic in their distribution, but a few are present in every colony which shows the other characteristics. The granulation of the cryptocyst is a distinctive feature, being fine and close and very even. That of *M. coriacea* is somewhat coarser and less close, and, over the greater part appears less regular owing to interruption by the more numerous pores.

The differences in dimensions and number of pores are evident to direct examination. Sample measurements and counts made by Miss Cook, as a trial, support these observations. They are based on a total of 30 zooecia and 16 ovicells from 4 colonies of *M. coriacea* from 4 different British localities; and 40 zooecia and 20 ovicells from 5 colonies of *M. normani* from 3 different British localities. Many more would be needed to obtain statistically reliable figures.

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[1] *M. coriacea* Johnston not Esper, see footnote above under *Membranipora hexagona.*

[2] See Hastings (forthcoming paper on *Hippothoa*).

MEASUREMENTS OF ZOOECIA AND OVICELLS. *M. coriacea:* Lz 0·40–0·70 mm., average 0·50 mm. lz 0·30–0·48 mm., average 0·39 mm. Lov 0·18–0·25 mm., average 0·22 mm. lov 0·24–0·32 mm., average 0·28 mm. *M. normani*: Lz 0·30–0·47 mm., average 0·39 mm. lz 0·21–0·40 mm., average 0·32 mm. Lov 0·12–0·17 mm., average 0·15 mm. lov 0·15–0·26 mm., average 0·21 mm.

NUMBER OF CRYPTOCYSTAL PORES. *M. coriacea*: 30–60, average 45. *M. normani*: 12–15, average 20.

On the evidence available to me, *M. normani* is distinct from *M. coriacea*. The two are easily recognizable and there is no intergrading.

Species of *Micropora* with avicularia from (a) Port Phillip, Victoria (Bracebridge Wilson Collection) and (b) Madeira (Norman Collection) and the Mediterranean (Busk Collection) have been identified with *M. coriacea*, but it seems likely that both species are distinct from both *M. coriacea* and *M. normani*. *M. coriacea* s. lat. needs full revision.

To sum up, *M. normani* differs from British *M. coriacea* s. str. in the presence of avicularia, the smaller zooecia, the smaller number of cryptocystal pores, the whitish, granular opercula and the absence of the ridge (sometimes umbonate) on the ovicell which may, however, have a small umbo.

The distribution of *M. normani* is Armorican (see Lagaaij, 1952 : 11), extending from Spain to the western and south-western shores of the British Isles.

CHARACTERS OF THE GENUS *Micropora*. *M. coriacea* is the type-species of *Micropora* Gray (1848 : 115), see Brown (1952 : 125). If it is confirmed that British *M. coriacea* s. str. is without avicularia, generic definitions, e.g. those of Brown (1952) and Bassler (1953), will have to be emended by adding the words " when present " to the characterization of the avicularia.

Brown (1952 : 126) noted that the avicularia in *Micropora* are not adventitious, as described by Harmer, but are what we now term interzooecial. This can be seen in the neotype and other specimens of *M. normani*.

The ovicells of both *M. coriacea* and *M. normani* are not endozooecial (as stated by Levinsen, 1909 : 162), but recumbent.[1] This can be observed by examining the growing edge of the colony where the complete ovicell projects at the distal end of the fertile zooecium before the distal and distal-lateral zooecia appear. As these zooecia develop the ovicell becomes surrounded by them and thus imbedded in the zoarium.

Spines are usually stated to be absent in *Micropora*, but a single specimen of a species (undescribed?) from Algeria (1869.10.6.6) has, on many zooecia, a pair of stout distal spines, rather widely set (being about opposite to the proximal corners of the distal zooecium). More rarely there is one median distal spine.

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[1] The term *recumbent* was introduced by Canu & Bassler (1917 : 66), see Brown (1954 : 244, footnote).

Salicornaria clavata Busk

Salicornaria clavata Busk (part), 1884 : 88, pl. XII, figs. 8, 8c, text-fig. 5 (not figs. 8a, b, St. 162 Bass Strait = *C. australis*).
Cellaria australis MacGillivray Waters (part), 1888 : 16, pl. 11, figs. 1–4.
Cellaria clavata (Busk) Hastings, 1947 : 236.

DISTRIBUTION. S. Indian Ocean.

LECTOTYPE, chosen here : 1887.12.9.395 part. Challenger St. 151, Heard Island.

PARALECTOTYPES. 1887.12.9.391, 396 ; 1899.7.1.1545 ; 1934.2.16.34. St. 149D, Kerguelen. 1882.7.29.75 ; 1887.12.9.389 ; 1899.7.1.1550 ; 1934.2.16.35. St. 151, Heard Island. 1887.12.9.390, 393 ; 1899.7.1.1551. Prince Edward Island.

OTHER MATERIAL. St. 149D (1963.2.12.200) ; St. 151 (1963.2.12.243). Both specimens received from Dundee Museum. No evidence as to whether named by Busk.

REMARKS. Waters accepted Busk's treatment of the Australian and South Indian Ocean forms as one species, and used the earlier name *Cellaria australis* MacGillivray. Hastings distinguished *Cellaria clavata* (Busk) from *C. australis*[1] but did not choose a lectotype. A colony from St. 151 is now chosen, this being the station from which Busk's figured material of this species was obtained.

The colony from St. 149D (1887.12.9.396) is large, has a mass of anchoring rootlets forming a short stalk, and very numerous branches which, in its dry state, are close together and more or less parallel to each other,[2] as if growing vertically. The rootlets attaching the lateral branches to the parent branches are brittle in their dry state, and many branches have fallen off, but the remaining colony is 93 mm. tall and 42 mm. × 35 mm. at its thickest point. The longest branch (broken at the tip) measures 78 mm. The average diameter of the branches is 2 mm.

The figures of the chitinous parts given by both Busk and Waters represent true *C. clavata*. The opercula of *C. australis* differ from those of *C. clavata* in their less conspicuous " foramina ", which are not visible at all focal levels, and in the absence of the granulations shown in Busk's and Waters's figures. In *C. australis* the opercula are very slightly shorter and distinctly narrower. Miss Cook has measured chitinous parts mounted by Busk (the figures being necessarily based on rather few measurements) :

C. australis, 1899.7.1.1546. Lo 0·08–0·09 mm., average 0·085 mm. lo 0·09–0·105 mm., average 0·10 mm.

C. clavata, 1899.7.1.1545. Lo 0·085–0·10 mm., average 0·095 mm. lo 0·13–0·16 mm., average 0·15 mm.

C. clavata, 1882.7.29.75. Lo 0·12–0·14 mm., average 0·13 mm. lo 0·12–0·14 mm., average 0·13 mm.

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[1] They differ in areolation and jointing, and in the presence of cryptocyst ridges in *C. clavata*.

[2] The flexibility of the rootlet attachment of the lateral branches, before drying, has made this possible.

The third of these preparations, in which the opercula are as long as wide, was made from a fertile branch and has remarkably large embryos throughout.

The mandibles of *C. australis* are considerably wider than those of *C. clavata*, being wider than the operculum :

C. clavata, l mand. 0·10–0·11 mm., average 0·105 mm.
C. australis, l mand. 0·14–0·17 mm., average 0·155 mm.

The specimens of *C. clavata* from Prince Edward Island differ in their longer zooecia and in the areolation of the fertile zones (Hastings, 1947 : 237). The opercula, measured from those mounted by Busk, resemble those of *C. clavata* from the other stations in width, but are shorter :

1899.7.1.1551. Lo 0·09–0·11 mm., average 0·10 mm. lo 0·11–0·13 mm., average 0·115 mm.

The width of the mandibles is the same as for those from the other stations quoted above.

Siphonoporella nodosa Hincks

Siphonoporella nodosa Hincks, 1880*b* : 90, pl. XI, fig. 10 ; Harmer, 1900 : 231 ; Levinsen, 1909 : 170, pl. VI, figs. 2a, b.

DISTRIBUTION. Australia.

LECTOTYPE, chosen here : Specimen figured by Hincks, E.C. Jelly Collection, Manchester Museum. Australia.

PARALECTOTYPE. 1899.5.1.685, Hincks Coll., mounted by Jelly. Australia.

OTHER MATERIAL. Australia (Bracebridge Wilson Coll., 1897.5.1.582, mounted by Jelly, but not known to have been examined by Hincks) ; Western Australia (E. Lempriere Coll., 1948.3.12.2, on *Metamastophora plana*).

REMARKS. The figured zooecia are recognizable in the Manchester Museum specimen, and I have therefore chosen it as lectotype. Levinsen figured a specimen resembling the lectotype in having a well developed gymnocyst with usually more than 2 nodules.

In the British Museum specimens the gymnocyst of nearly all the zooecia is much narrower, usually with only 2 nodules, one in each proximal corner. In the paired daughter-zooecia, at the bifurcation of the series, one or both the inner[1] nodules is reduced or absent. In each Jelly specimen there are, however, a few zooecia with a wider gymnocyst and more numerous, more irregular nodules, and these are more frequent in 1948.3.12.2. In the latter specimen the zooecia with narrow gymnocyst often have a small median nodule in addition to the two in the corners.

The most recent comments on *Siphonoporella* have been made by Silén (1941 : 62) and Cook (1964 : 57). References to some earlier work are to be found in both these papers. Canu & Bassler (1929 : 149) described a species from the Philippines. *S. nodosa* is the type-species of the genus.

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[1] i.e. the nodule in the corner next to the other zooecium of the pair.

4. THE GENUS *HIPPOPLEURIFERA* AND SOME OF ITS SPECIES

Hippopleurifera Canu & Bassler

Hippopleurifera Canu & Bassler, July 1925 : 679. (*Hippopleurifera biauriculata* Reuss, 1847 [*sic*] listed, with full reference.)

Hippopleurifera Canu *nov.* Canu & Lecointre, 1925 : 9 (Genus only, listed.)

Hippofleurifera [*sic*] Milne-Edwards, 1836 ; Canu, 1926 : 764. (*H. sedgwicki* Milne-Edwards, 1836 listed.)

Hippopleurifera new genus Canu & Bassler, 1927 : 7. (Defined, with *Eschara sedgwicki* Milne-Edwards designated as type.)

Hippopleurifera Canu & Bassler, 1927 ; Canu & Bassler, 1929 : 326. (Same definition and type as in 1927.)

Hippopleurifera nov. Canu & Lecointre, 1930 : 86. (Same definition, in French, and type as in Canu & Bassler, 1927.)

Hippopleurifera Canu & Bassler, 1927 : Bassler, 1935 : 127. (Listed with a reference to Canu & Bassler, 1929, and with *E. sedgwicki* as type.)

Hippopleurifera Canu ; Hastings, 1949 : 524. (Discussed with *E. sedgwicki* as type.)

Hippopleurifera Canu & Lecointre, 1925 ; Vigneaux, 1949 : 96. (Same French definition and type as Canu & Lecointre, 1930.)

Hippopleurifera Canu & Bassler, 1925 ; Lagaaij, 1952 : 92. (Revised diagnosis with *Eschara biauriculata* Reuss named as type by monotypy.)

Hippopleurifera Canu, 1927 ; Bassler, 1953 : G 196. (Brief definition with *E. sedgwicki* as type.)

Hippopleurifera Canu & Bassler, 1924 ; Buge, 1957 : 265. (Redefined with *E. biauriculata* as type.)

Hippopleurifera Brown, 1958 : 65. (Footnote on priority of *E. biauriculata* as type-species.)

TYPE-SPECIES. It appears that the use of the name *Hippopleurifera* by Canu & Bassler in 1925 was a valid generic introduction, and that Lagaaij and Buge were right in taking *Eschara biauriculata* Reuss as the type by monotypy. It is therefore important to ascertain the characters of Reuss's species.

Hippopleurifera biauriculata (Reuss)

(Plate 1, figs. 1–3).

Eschara biauriculata Reuss (part), 1848 : 66, pl. VIII, fig. 15 ; Manzoni, 1877 : 11, pl. IX, fig. 29.

Hippopleurifera biauriculata Reuss Canu & Bassler, 1925 : 679. (Listed.)

DISTRIBUTION. *Miocene*, Austria and Hungary. (Leithakalk at Eisenstadt, Mörbisch and Kroisbach bei Oedenburg, see bed no. 6, Reuss p. 4).

LECTOTYPE, chosen here : 1859.L.748, Mineralien-Kabinet of Naturhistorisches Museum, Vienna. Bryozoen Sand, Eisenstadt. Specimen figured by Manzoni.

EXAMINATION OF SYNTYPES. The syntype material, kindly lent by the Naturhistorisches Museum, Vienna, consists of two small, escharan fragments, together in one tube, with an original label. They belong to distinct species. One of them (Pl. 1, figs. 4, 5) is referable to *Hippopleurifera sedgwicki* (Milne-Edwards, see below). The other (Pl. 1, figs. 1–3) is evidently the form figured by Reuss, as it shows the

" biauriculate " character. This specimen is now chosen as the lectotype of *Eschara biauriculata.*

Comparison with my Pl. 1, fig. 1 will show that the detailed agreement (zooecium by zooecium, and ovicell by ovicell) leaves no possible doubt that the lectotype specimen is represented (in mirror image) in Manzoni's figure. There are some points for criticism in his figure : (1) the scattered pores on the marginal zooecium are shown as arranged in regular rows, (2) the areola-like pores round the ovicell are exaggerated, and the frontal sculpture omitted, (3) although some variation in the size of the avicularia is shown, their shape is not satisfactorily represented.

Description of lectotype (Pl. 1, figs. 1–3). *Specimen* a bilaminar fragment (5·0 mm. × 3·1 mm.) including part of edge of frond. Zooecia alike on both flat surfaces and continuous over marginal surface.

Zooecia with median, suboral mucro and porous frontal wall, pores separated by smooth bars. Peripheral pores round, grading into a few oblique groove-like pores which converge on mucro (evidently a porous pleurocyst.)

Spines absent.

Orifice round with a very slight demarcation of a large anter and a small poster.

Avicularia one on each side of orifice, either both small (as in Reuss's figure) or one enlarged. Small avicularia on rim of orifice directed outwards with bluntly pointed rostrum. Large avicularia lying beside orifice and directed distally, mostly, but not all, on fertile zooecia, rostrum spatulate with straight or (in the largest avicularia) concave sides, proximal end of avicularium raised.

Ovicells hyperstomial, their secondary covering continuous with pleurocyst of distal zooecium. Secondary cover with two large fossae, or with irregular smaller pits and protuberances (see two ovicells side by side in Pl. 1, figs. 1 and 3).

Remarks. *H. biauriculata* (Pl. 1, figs. 1–3) has more in common with *H. pulchra* Manzoni (see Hastings, 1949, pl. XII, fig. 2) than with *H. sedgwicki* (see Pl. 1, figs. 4, 5, and Hastings, 1949, pl. XII, fig. 1). It resembles *H. pulchra* in the greater extent of the porous pleurocyst (*H. sedgwicki* usually having a small area without pores behind the orifice) ; in the less pronounced division of the orifice into anter and poster ; and in the details of the secondary calcification of the ovicell.

H. biauriculata differs from *H. pulchra* in the smoothness of the frontal wall between the pores, which are larger ; and in the shape and position of the avicularia. In *H. pulchra* the granulations and projections on the areas between the pores are the noticeable feature of the frontal wall. Spines, which are absent in the small specimen of *H. biauriculata*, are conspicuous in both the other species. The three species appear to be congeneric.

A phase with two fossae is also seen in the ovicells of most of the American Early Tertiary species referred to *Hippomenella* by Canu & Bassler (1920 : 379 *et seq.*). Brown (1949 : 517) rejected these species from *Hippomenella*. Hastings (1949 : 525) transferred some of them to *Hippopleurifera*, and Brown (1958 : 65) placed some in *Trigonopora* which also has fossae.

Hippopleurifera pulchra (Manzoni)

Cellepora pulcra [*sic*] Manzoni (Michelotti MS.), 1870 : 336, 338, pl. IV, fig. 20.
Hippodiplosia granulosa Canu, 1916 : 327, pl. III, figs. 7, 8.
Lepralia soulieri Calv.; Waters, 1926 : 429. (Development of pleurocyst.)
Not *Mucronella soulieri* Calvet ; O'Donoghue & de Watteville, 1939 : 28. (Record only.)
Hippopleurifera pulchra (Manzoni) Hastings, 1949 : 521, pls. XII, figs. 2–4, XIII, figs. 1, 1a, 2, 2a (Synonymy) ; Gautier, 1962 : 189.
Hippopleurifera granulosa Canu ; Vigneaux, 1949 : 97. (Record only.)

DISTRIBUTION. *Recent*, Mediterranean. *Miocene*, Italy ; Sicily ; Austria ; France.

REMARKS. *Hippodiplosia granulosa* Canu is clearly recognizable, from Canu's figure, as a synonym of *Hippopleurifera pulchra*. It is one of the two genosyntypes of *Hippodiplosia* Canu (1916 : 326). As Hastings (1930 : 724) chose the other genosyntype as genolectotype, the status of *Hippodiplosia* is not affected by this synonymy.

The specimen from Alexandria (1963.8.2.27), recorded by O'Donoghue & de Watteville as *Mucronella soulieri*, is referable to *Schizoporella errata* (Waters), for which see Gautier (1962 : 149).

Hippopleurifera sedgwicki (Milne-Edwards)

(Pl. 1, figs. 4, 5)

Eschara sedgwicki Milne-Edwards, 1836 : 330 (sep. p. 10), pl. 10, figs. 5, 5a.
Eschara biauriculata Reuss (part), 1848 : 66. (Not pl. VIII, fig. 15.)
Hippopleurifera sedgwicki (Milne-Edwards) ; Buge, 1957 : 265. (Synonymy.)

DISTRIBUTION. *Pliocene*, Europe and North Africa (see Buge). *Miocene*, Austria.

REMARKS. The paralectotype of *Eschara biauriculata*, referred above to *Hippopleurifera sedgwicki*, is from Eisenstadt, and extends the known range of *H. sedgwicki*, both geologically and geographically.

Buge redescribed this species.

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6. SUMMARY

Examination of type-material of a number of species has yielded information on their taxonomic status, distribution, structure, etc. The type-species of the genus *Hippopleurifera* is included, and one of the Siboga species of *Sclerodomus* is reconsidered. *Membranipora hexagona* Busk was based on a single, mutilated specimen of an unidentifiable, non-membraniporine species.

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PLATE 1

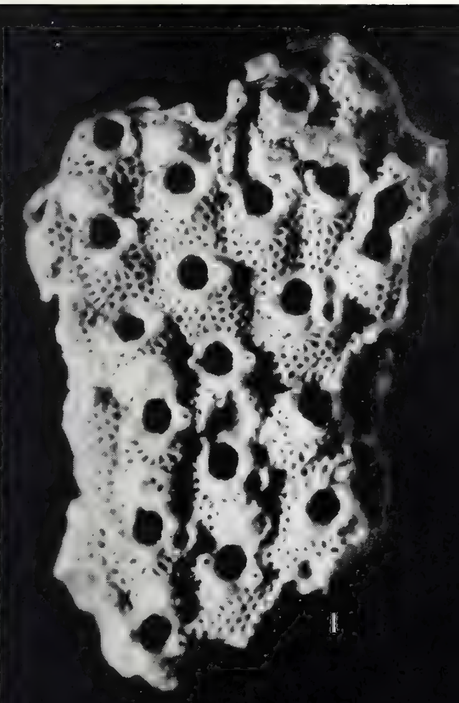
FIGS. 1–3. *Hippopleurifera biauriculata* (Reuss).

FIGS. 1, 2. The two faces of the bilaminar lectotype. Fig. 1. The face figured by Manzoni, showing the edge of the frond (left) and stages in the secondary calcification of the ovicells.

FIG. 3. Part of fig. 1 enlarged, showing two biauriculate fertile zooecia, and two with one of the avicularia large and spatulate ; variation in older, secondarily calcified ovicells ; and parts of the outwardly facing zooecia at the edge of the frond.

FIGS. 4, 5. *Hippopleurifera sedgwicki* (Milne-Edwards). The two faces of the bilaminar paralectotype of *H. biauriculata* (Reuss.).

Figs. 1, 2, 4, 5. × 16. Fig. 3. × 36.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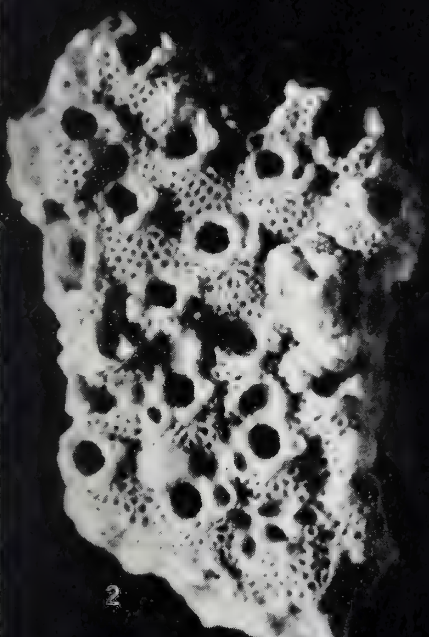
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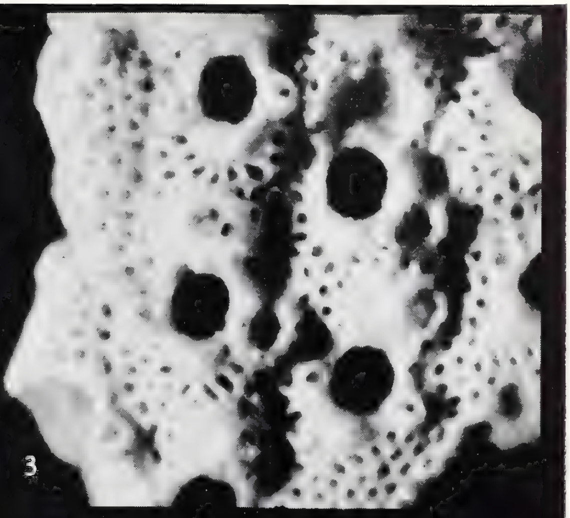
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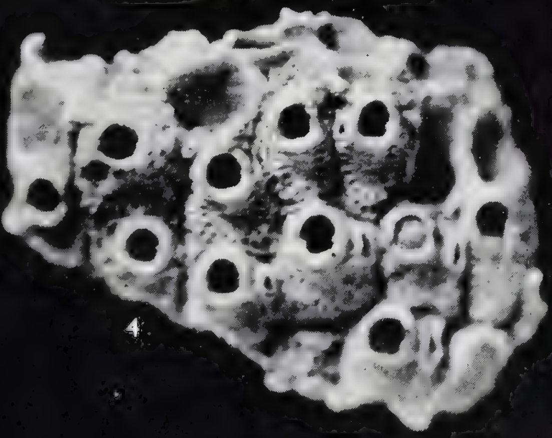
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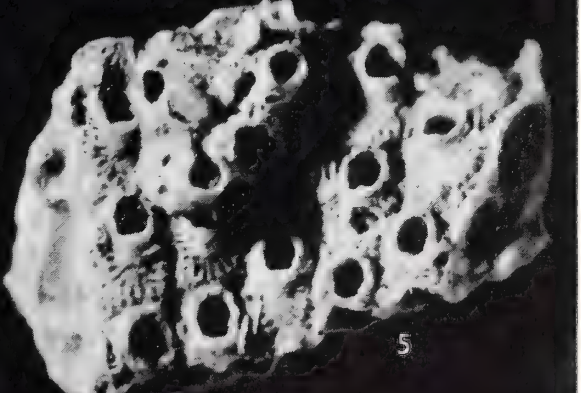
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MARINE NEMATODES FROM DURBAN, SOUTH AFRICA

WILLIAM G. INGLIS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 14 No. 4
LONDON: 1966

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Pp. 79–106 ; 47 *Text-figures*

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MARINE NEMATODES FROM DURBAN, SOUTH AFRICA

By WILLIAM G. INGLIS

SYNOPSIS

Ten new species and three new genera of free-living marine nematodes are described from the Durban area of the Republic of South Africa, thus : *Platycoma sudafricana* sp. nov. is characterized by an arrow-head-shaped flap over the amphid and, possibly, by some features of the male tail ; *Trileptium longisetosum* sp. nov. is similar to *T. ayum* Inglis, 1964 but differs in the distribution of the cervical setae and the form of the spicules ; *Mesacanthion frica* sp. nov. is characterized by the form of the spicules which have long ventro-posteriorly directed processes on their anterior ends ; *Epacanthion oliffi* sp. nov. is a short spiculed form characterized by lacking a gubernaculum and pre-cloacal supplement and having many cervical setae in the male ; *Rhabdodemania dura* sp. nov. is characterized by a lack of ventro-lateral onchia and the shape of the spicules ; *PHERONOUS ogdeni* gen. et sp. nov. of the Ironidae is characterized by a lack of caudal glands and papilla-like cephalic sense organs ; *Metoncholaimus murphyi* sp. nov. is characterized by having one pore to the demanian system, extremely long spicules and a few long circum-cloacal setae ; *WIESONCHOLAIMUS mawsonae* gen. et sp. nov. of the Oncholaimidae is characterized by long, equal, ventro-lateral onchia and a short dorsal onchium, a long stout tail, very long slim spicules and a large gubernaculum, and the presence of a demanian system ; *PLECTOLAIMUS juliani* gen. et sp. nov. of the Leptolaimidae is characterized by six distinct lips, ventral onchia-like structures at the anterior end of the oesophagus and a distinct bulb-like region with tiny valves at the posterior end of the oesophagus ; *Bathylaimus deconincki* sp. nov. is characterized by a large relatively posterior amphid and by the shape of the spicules and gubernaculum. *Hyalacanthion* Wieser, 1959 is a synonym of *Epacanthion* Wieser, 1953 because *E. butschlii* (Southern, 1914), type species of *Epacanthion*, has typical *Hyalacanthion* mandibles. As a further consequence it is argued that subdivision of the families of the Enoploidea is not yet possible, in spite of De Coninck's recent attempt, particularly as De Coninck refers *Hyalacanthion* to one subfamily and *Epacanthion* to another.

INTRODUCTION

THREE samples of free-living marine nematodes were sent to me by Dr. W. D. Oliff, South African Council for Scientific and Industrial Research, National Institute for Water Research. These samples contain ten species, all of which are described below as new, referable to ten genera, of which three are new. As usual only those species represented by males in good condition are described. The species were collected from the following localities :

Beach sand in the surf zone from the Durban area on 10.viii.1964. (Collection number : B8n8.)

1 ♂. *Bathylaimus deconincki* sp. nov.
2 ♂, 9 ♀. *Epacanthion oliffi* sp. nov.

1 ♂. *Mesacanthion frica* sp. nov.
3 ♂, 1 ♀. *Metoncholaimus murphyi* sp. nov.
12 ♂, 16 ♀, 4 larvae. *Pheronous ogdeni* sp. et gen. nov.
2 ♂. *Platycoma sudafricana* sp. nov.
1 ♂. *Plectolaimus juliani* sp. et gen. nov.
3 ♂, 1 ♀, 12 larvae. *Trileptium longisetosum* sp. nov.

Sediments in the mouth of Durban Harbour (polluted) on 20.vi.1964. (M23n4.)

11 ♂, 6 ♀, 1 larva. *Rhabdodemania dura* sp. nov.
6 ♂, 12 ♀. *Wiesoncholaimus mawsonae* sp. et gen. nov.

From the same locality as M23n4 on same date (M23n11).

2 ♂, 11 ♀, 8 larvae. *Wiesoncholaimus mawsonae* sp. et gen. nov.

SYSTEMATIC CONSIDERATIONS

De Coninck (1965) has made a heroic attempt to provide a more reasonable classification of the free-living nematodes in which he divides the Superfamily Enoploidea into six families and fifteen subfamilies. Although some of these divisions appear to be reasonable others are certainly not at present acceptable. For example he still recognizes Thoracostomopsidae as a distinct family with only one genus *Thoracostomopsis*. But this genus is only a somewhat modified Enoplidae which is well within the ranges of variation shown by the genera currently referred to that family. Further, De Coninck refers *Hyalacanthion* Wieser, 1959 to one subfamily of the Enoplidae (Enoploidinae) and refers *Epacanthion* Wieser, 1953 to another (Enoplolaiminae). But I show below that the genera cannot be separated.

I argued recently (Inglis, 1964*) that *Enoplus* is a highly evolved form, while De Coninck treats it as a form ancestral to all the genera he refers to the family Enoplidae, but gives no indication of the origins of *Enoplus* itself. I have further argued, and still do, that the Enoplidae can be considered as having arisen from the genera commonly referred to the Family Phanodermatidae. In the latter family buccal rods appear to be commonly present and it is easy to imagine how, by a process of increased sclerotization, the region of the inner surface of the lip between these rods could become thickened to produce the mandibles so characteristic of the Enoplidae. Within the Enoplidae several lines can be crudely recognized along each of which the mandibular : onchial complex has been modified in a different way. The problem is not that of interpreting the components of each line but simply that we do not have enough information to make such an attempt worth while. We can only await the collection of more data and until then I still propose to recognize no groups other than Families and Genera.

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* In this paper read cephalic ventricle for cephalic vesicle throughout.

DESCRIPTIVE SECTION

Family **LEPTOSOMATIDAE**

Platycoma sudafricana sp. nov.

(Text-figs. 1–6)

MATERIAL STUDIED. 2 ♂. Beach sand in the surf zone. Near Durban, Republic of South Africa (B8n8). B.M. (N.H.), Reg. Nos. 1965.961–962.

A	B	C	Body length (mm.)
146·38	8·21	56·10	10·1
144·74	8·53	68·75	11·1

MEASUREMENTS (in mm., in order of body lengths)

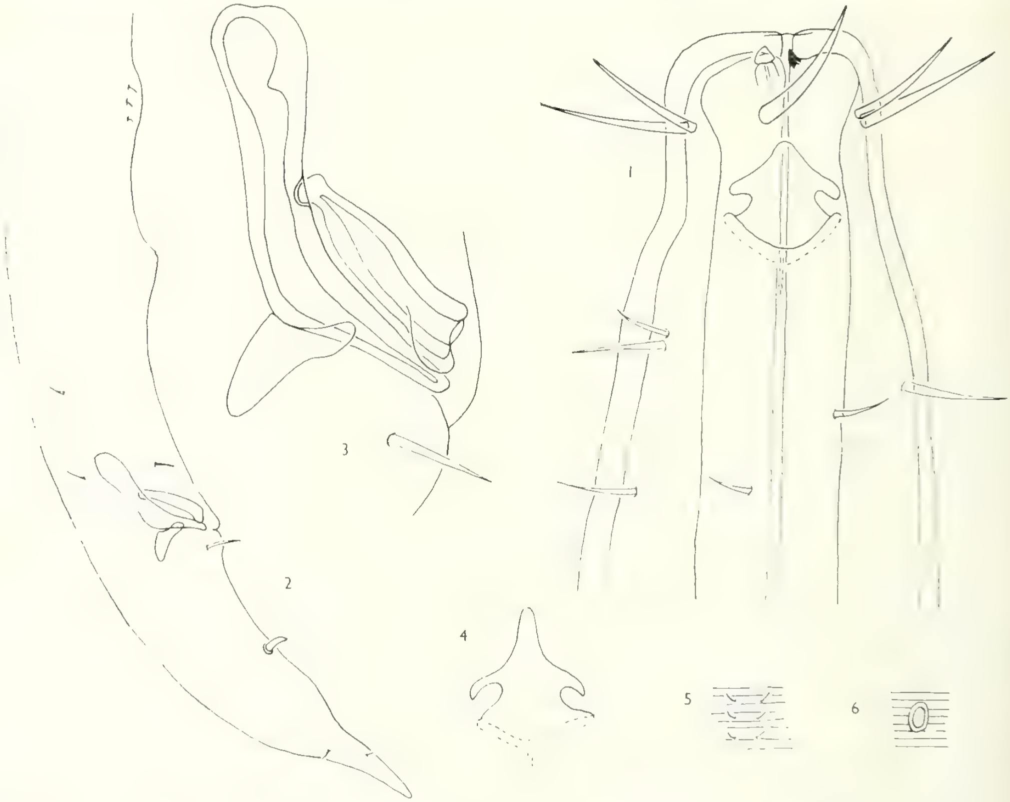
Body breadth: 0·069; 0·076. Oesophagus length: 1·23; 1·29. Diameter of head: 0·031; 0·029. Length of cephalic setae (long/short): 0·023/0·018; 0·023/0·018. Distance from anterior end of body to posterior edge of amphid: 0·026; 0·027. Length of cervical setae: 0·014–0·018; 0·014–0·017. Distance of nerve ring from anterior end of body: 0·30; 0·29. Length of spicules: 0·163; 0·165. Length of lateral piece of gubernaculum: 0·033; 0·035. Length of apophosis of gubernaculum: 0·015; 0·014. Distance of first pre-cloacal supplement anterior to cloacal opening: 0·087; 0·122. Distance of second pre-cloacal supplement anterior to cloacal opening: not measured, tail too curved; 0·198. Length of tail: 0·18; 0·16. Cloacal diameter: 0·066; 0·060.

The anterior end of the body is set off as a constricted region starting about the level of the posterior edge of the amphids (Text-fig. 1). The mouth opening is simple, tri-radiate and leads almost immediately into the oesophagus which carries three small wholly cuticular onchia on each sector (Text-fig. 1). The cephalic sense organs lie in two circles of which the inner consists of six prominent papillae while the outer consists of ten setae of which six are long and four are shorter (Text-fig. 1). There are many long cervical setae. The amphids are prominent with a large arrow-head-like flap of cuticle developed from their anterior edge (Text-figs. 1 and 4). The oesophagus is long and simple in outline.

The tail bears a pair of prominent spike-like setae about half-way along its length and a long but slim seta just posterior to the cloacal opening (Text-fig. 2). There is no spinerette and there are no caudal glands. On the mid-ventral surface of the body anterior to the cloacal opening there are two pre-cloacal supplements (Text-fig. 2) of which the more posterior (Text-fig. 6) is a rounded cap-like structure resembling a Type-1 campaniform organ (Inglis, 1963) while the more anterior (Text-fig. 5) is a raised area on which are located three pairs of short, stoutish setae.

The spicular : gubernacular complex is double. That is, all the structures shown in the figure (Text-fig. 3) are represented by exactly equivalent structures on the other side of the body and they are in no way connected across the mid-line of the body. Further, the entire complex appears to form one functional unit. Here I interpret the structures as Gerlach (1955) does and not as he re-interprets them later

(1959). That is I consider the largest L-shaped structure to be the spicule which is enfolded posteriorly by a slightly triangular-shaped gubernacular apophosis. The most interesting feature is the relationship between the spicule and the rod-like structure bordering it anteriorly (considered a spicule by Gerlach (1959)). This rod swells towards its distal end where it bears a lateral flange which enfolds the distal end of the spicule while the same rod swells to form a slight knob proximally which fits into a socket in the spicule.



Figs. 1–6. *Platycoma sudafricana* sp. nov. Fig. 1. Lateral view of head. Fig. 2. General lateral view of male tail. Fig. 3. Detail of spicular : gubernacular complex from right side. Note the articulation between the spicule and the anterior part of the gubernaculum. Fig. 4. Variant form of amphid. Fig. 5. Ventral detail of more anterior pre-cloacal supplement. Fig. 6. Ventral detail of more posterior pre-cloacal supplement.

Discussion

This genus appears to be characterized by the peculiar modification of the spicular apparatus, the presence of pre-cloacal supplements, the presence of the pair of stout, spine-like setae on the tail and in lacking caudal glands. In addition the head is highly characteristic with three small onchia and the marked sexual dimorphism of the amphids. In this respect the present species resembles *P. africanus* (Gerlach,

1959) but differs from it in the arrow-head-like form of the amphidial flap. *P. sudafricana* is also, possibly, characterized by the number and form of the pre-cloacal supplements and the form of the spicular : gubernacular complex.

Platycoma is very similar to *Platycomopsis* Ditlevsen, 1926 but this latter genus does not show any sexual dimorphism of the male amphids, and the male apparatus is more typical with long spicules and a short anterior part to the gubernaculum. This does, however, appear to represent a simpler version of the apparatus found in *Platycoma* and is one of the reasons for the interpretation I advance above. In addition *Platycomopsis* does not have the pair of spine-like setae on the male tail which is such a characteristic feature of the species referred to *Platycoma*.

Trileptium longisetosum sp. nov.

(Text-figs. 7–9)

MATERIAL STUDIED. 3 ♂, 1 ♀, 12 larvae. Beach sand in the surf zone. Near Durban, Republic of South Africa (B8n8). B.M. (N.H.) Reg. Nos. 1965.963–972.

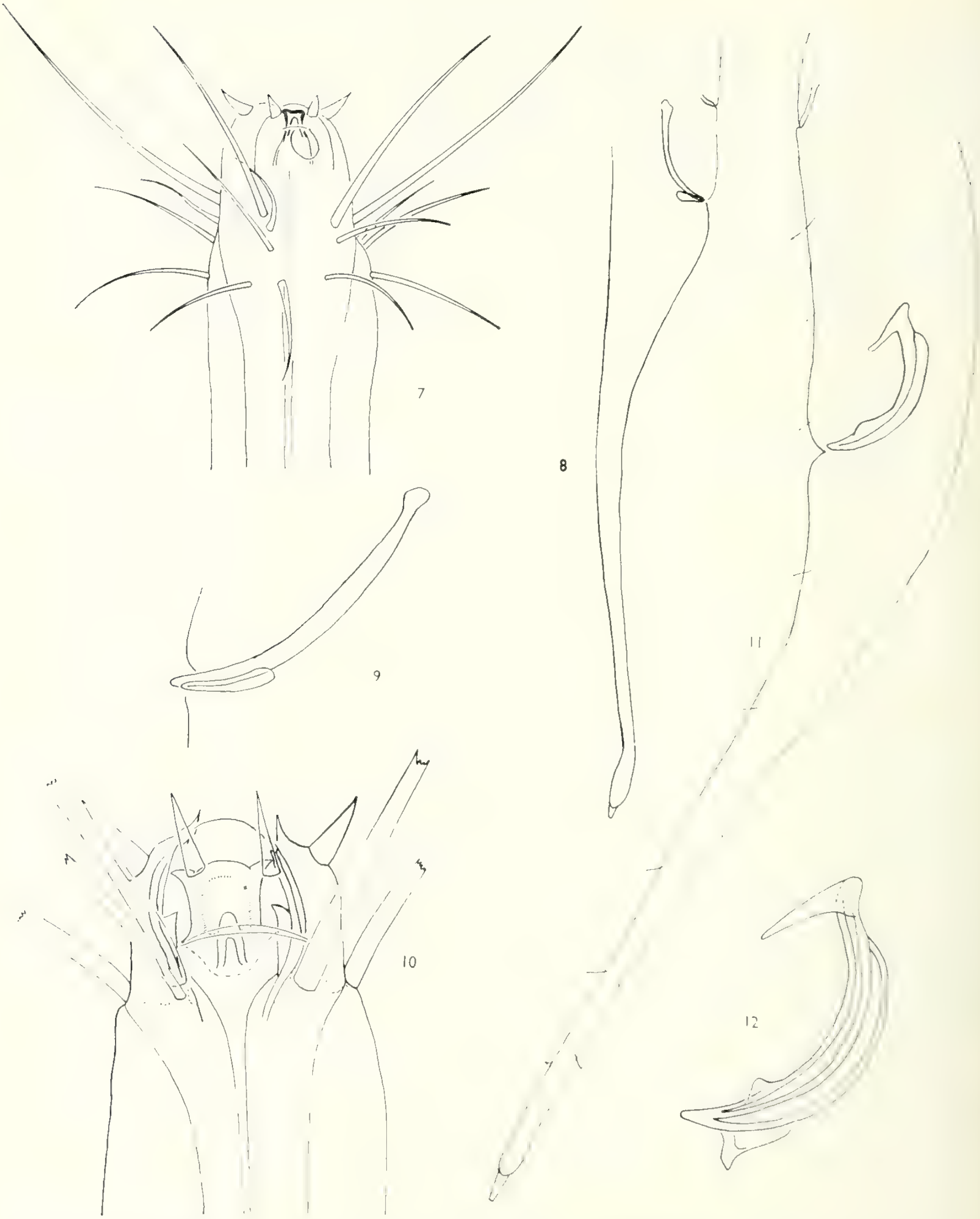
	A	B	C	V	Body length (mm.)
Males	10·64	5·63	22·69	—	4·68
	10·65	5·10	24·50	—	4·90
Female . . .	8·10	6·51	22·05	52·90	3·97
Larva	8·54	5·69	24·12	—	4·10

MEASUREMENTS (in mm. in order of body lengths)

MALES : Body breadth : 0·044 ; 0·046. Oesophagus length : 0·83 ; 0·96. Diameter of head : 0·017 ; 0·018. Length of cephalic capsule : 0·036 ; 0·034. Diameter of cephalic capsule at posterior end : 0·019 ; 0·022. Length of longest cephalic setae : 0·040 ; 0·039. Length of cervical setae : 0·018–0·020 ; broken. Distance of nerve ring from anterior end of body : 0·19 ; 0·21. Length of spicules : 0·047 ; 0·052. Length of gubernaculum : 0·018 ; 0·016. Length of pre-cloacal supplement : 0·0065 ; 0·0065. Distance of pre-cloacal supplement anterior to cloacal opening : 0·038 ; 0·040. Length of tail : 0·21 ; 0·20. Cloacal diameter : 0·036 ; 0·040.

FEMALE : Body breadth : 0·049. Oesophagus length : 0·61. Diameter of head : 0·020. Length of cephalic capsule : 0·022. Diameter of cephalic capsule at posterior end : 0·025. Length of longest cephalic setae : 0·066. Length of cervical setae : 0·008. Distance of nerve ring from anterior end of body : 0·16. Length of tail : 0·18. Anal diameter : 0·036. Distance of vulva from anterior end of body : 2·1.

LARVA : Body breadth : 0·048. Oesophagus length : 0·72. Diameter of head : 0·020. Length of cephalic capsule : 0·023. Diameter of cephalic capsule at posterior end : 0·021. Length of longest cephalic setae : 0·042. No cervical setae. Distance of nerve ring from anterior end of body : 0·19. Length of tail : 0·17. Anal diameter : 0·043.



FIGS. 7–9. *Trileptium longisetosum* sp. nov. Fig. 7. Ventro-lateral view of head. Fig. 8. Lateral view of male tail. Fig. 9. Spicule and gubernaculum from the left. Figs. 10–12. *Mesacanthion frica* sp. nov. Fig. 10. Dorsal view of head. The cephalic setae are not drawn in full because of their great length. Fig. 11. Lateral view of male tail. Fig. 12. Detail of spicule and gubernaculum (?) from the left.

The structure of the head is the same as that in *Trileptium ayum* Inglis, 1964 with three small onchia enclosed by three small mandibles. The setae of the inner circle of cephalic sense organs are very stout and prominent and the pouch of the cephalic slit is rounded and very prominent (Text-fig. 7). The "cephalic setae" are numerous and consist of six very long setae followed by two shorter setae on the dorso- and ventro-lateral positions and by one on the lateral positions. In the males there is one circle of ten cervical setae (Text-fig. 7) while there are four, much shorter setae in the equivalent position in the females. In addition there are a number of long, thin setae on the anterior end of the body which become sparser posterior to the nerve ring. Such setae measure 0·009–0·013 mm. in length.

The tail is long and narrow in both sexes and a very small rod-like pre-cloacal supplement is present on the ventral surface of the male anterior to the cloacal opening (Text-fig. 8).

The spicules are equal and identical with slightly cephalate proximal ends and bluntly rounded distal tips. The gubernaculum is simple and lies very close to the spicules (Text-fig. 9).

Discussion

This species is most similar to *T. ayum* Inglis, 1964 but differs from it in the number and distribution of the cervical setae and the short spicules. It appears to differ most markedly from all the other known species in having three onchia and a pre-cloacal supplement in the male.

Mesacanthion frica sp. nov.

(Text-figs. 10–12)

MATERIAL STUDIED. 1 ♂. Sand in surf zone. Near Durban. Republic of South Africa (B8n8). B.M. (N.H.) Reg. No. 1965.1011.

A	B	C	Body length (mm.)
42·31	3·75	0·07	1·65

MEASUREMENTS (in mm.)

Body breadth: 0·039. Oesophagus length: 0·44. Length of cephalic setae (anterior/longer posterior/shorter posterior): 0·013/0·096/0·051. Depth of cephalic capsule (?): 0·026. Diameter of cephalic capsule at posterior edge: 0·026. Distance of nerve ring from anterior end of body: 0·139. Length of body setae about level of nerve ring: 0·016. Length of spicules: 0·040. Length of pre-cloacal supplement: 0·012. Distance of pre-cloacal supplement anterior to cloacal opening: 0·078. Length of tail: 0·182. Cloacal diameter: 0·036.

The single specimen is in a rather poor condition so that some details cannot be reliably assessed. Nevertheless sufficient detail can be made out to warrant its description in view of the peculiar features it shows. The cephalic sense organs are very long and those of the posterior circle appear to lie about the posterior edge of the cephalic capsule. This is, however, uncertain and is suggested largely on the basis of the shape of the anterior end of the body (see Text-fig. 10). The mandibles are prominent but fairly lightly developed and show no indication of any mandibular rods as in the species I refer elsewhere to *Mesacanthion* (Inglis, 1964). In addition, the shape of the anterior edge of the mandibles is different resembling the conditions in *Africanthion* in that their ends are directed towards the inter-labial spaces rather than inwards towards the mandibular cavity. The onchial plate is very poorly developed with the onchia projecting just anterior to the mandibular ring.

The tail is long and slim and a small, rod-like, pre-cloacal supplement is present (Text-fig. 11). The most remarkable feature of the specimen is the form of the spicules (Text-fig. 12), which possess a long narrow ventrally-posteriorly directed process on their anterior ends; are in addition stout with a lateral bump near their posterior ends and appear to have a median central ridge running their full length. There is (?) a small gubernaculum, although its presence is uncertain.

Discussion

This species is characterized by the form of the spicules with the massive process on their anterior ends. Otherwise the spicules resemble those in *Enoplolaimus crassidens* Ditlevsen, 1930.

Epacanthion oliffi sp. nov.

(Text-figs. 13–16)

MATERIAL STUDIED. 2 ♂, 9 ♀. Beach sand in surf zone. Near Durban, Republic of South Africa (B8n8). B.M. (N.H.) Reg. Nos. 1965.1004–1010.

	A	B	C	V	Body length (mm.)
Males	34·81	3·19	10·33	—	1·88
	38·36	3·10	10·14	—	2·11
Females	25·34	3·49	11·64	58·92	1·85
	32·07	2·88	12·10	61·73	1·96
	32·58	3·16	8·98	58·42	2·02

MEASUREMENTS (in mm., in order of body lengths).

MALES: Body breadth: 0·054; 0·055. Oesophagus length: 0·59; 0·64. Diameter of cephalic capsule at posterior end: 0·034; 0·041. Depth of cephalic capsule: 0·033; 0·039. Length of cephalic setae (anterior/long posterior): 0·015/0·036; 0·016/0·039. Length of cervical setae: in range 0·035–0·039 on both specimens. Distance of nerve ring from anterior end of body: 0·131; 0·140. Length of spicules: 0·028; 0·029. Length of tail: 0·182; 0·208. Cloacal diameter: 0·044; 0·046. Length of setae on tail and on general body surface: up to 0·039 mm.

FEMALES: Body breadth: 0·073; 0·058; 0·062. Oesophagus length: 0·53;

0·68 ; 0·64. Diameter of cephalic capsule at posterior end : 0·038 ; 0·039 ; 0·038. Depth of cephalic capsule : 0·039 ; 0·041 ; 0·042. Length of cephalic setae (anterior/long posterior/short posterior) : 0·017/0·034/0·015 ; 0·016/0·036/0·016 ; 0·017/0·033/0·015. Length of cervical setae : 0·032 ; 0·028 ; 0·035. Distance of nerve ring from anterior end of body : 0·162 ; 0·138 ; 0·165. Length of tail : 0·159 ; 0·162 ; 0·225. Anal diameter : 0·048 ; 0·044 ; 0·052. Distance of vulva from anterior end of body : 1·09 ; 1·21 ; 1·18.

The head is typically enoplid with three high, slim lips bearing distinct semi-lunar striations lying on an area bounded anteriorly by a curved line running posteriorly from the tips of the mandibles (Text-fig. 13). The major part of the remainder of the lips is also marked by striations which are much further apart. These conditions are exactly as described for *Enoploides* species (see Inglis, 1964, fig. 30). The mandibles are typical of the genus with what appear to be two parallel rods joined by a thin sheet of cuticle. As usual this is due to studying a curved solid structure in optical section. The anterior ends of the mandibles form well developed projecting hooks. The three equal onchia are rather small and lie posterior to the posterior edge of the mandibles and do not lie close within them as in *Hyalacanthion multipapillatum* Wieser, 1959.

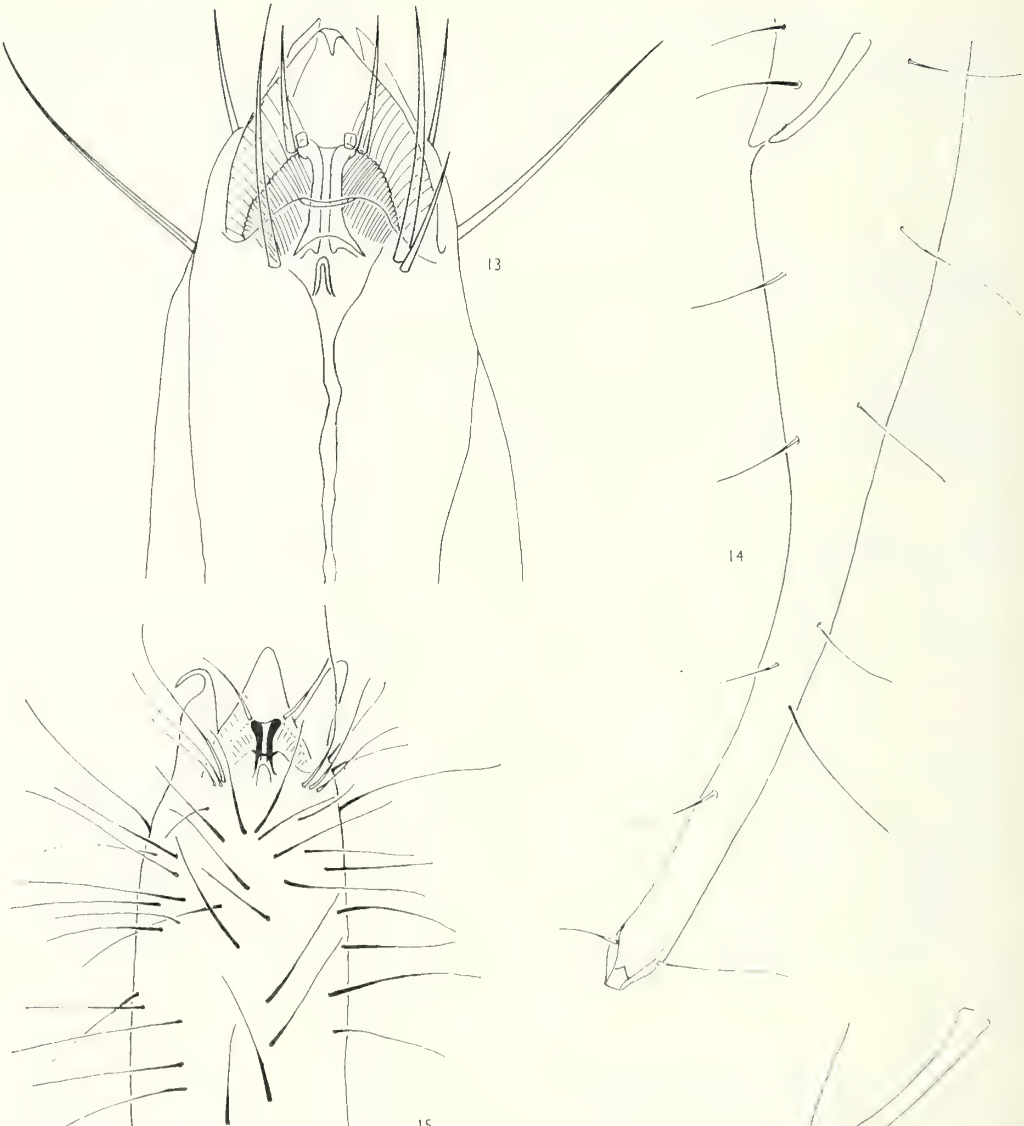
The cephalic setae are long and slim in both sexes with the more anterior pairs lying about the anterior end of the mandibles. Squarish blocks of specialized cuticle developed from the outer cuticle of head are closely associated with them (Text-fig. 13). In the females the outer setae are represented by six long setae and four short but in the males there are groups of three dorso- and ventro-laterally and two pairs laterally. In the females there are four long cervical setae but in the male the region of the body posterior to the cephalic capsule carries a very large number of long setae (Text-fig. 15). Setae become scarcer on the body posterior to about the level of the nerve ring but long setae occur sporadically over the entire length of the body.

The tail is somewhat blunt and stout in both sexes (Text-fig. 14). In the male there is no pre-cloacal supplement or gubernaculum. The spicules are short and stout with a series of serrations on their posterior ends (Text-fig. 16).

Discussion

Wieser (1959) erects a new genus *Hyalacanthion* for three species, *H. multipapillatum* Wieser, 1959 (type species) ; *H. pellucidus* (Savaljev, 1912) and *H. murmanicus* (Savaljev, 1912). This genus, as he points out, is very similar to *Epacanthion* ; the major differences between the two being that the mandibles in *Epacanthion* consist of two plates, separated by a lacuna, which are joined anteriorly by a narrow rod and the spicules are at least 2·5 anal diameters long while the mandibles in *Hyalacanthion* are plates joined by a thin transparent lamella and the long spicules are never less than 2·5 anal diameters long.

However Mawson (1958*a*) describes a new species, *Epacanthion brevispiculosum*, in which the spicules are considerably less than 2·5 anal diameters in length, and the species described above also has very short spicules. I do not think that *Epacanthion*



FIGS. 13–16. *Epacanthion oliffi* sp. nov. Fig. 13. Dorsal view of female head. Fig. 14. Lateral view of male tail. Fig. 15. Dorsal view of anterior end of male body. Fig. 16. Detail of spicule from the left.

can be separated from *Hyalacanthion* but the question is simplified by a study of the type male of *Enoplus butschlii* Southern, 1914 which Wieser (1953) selects as type species of *Epacanthion*. The structure of the lips and mandibles of this species is exactly the same as that described above for *E. oliffi*. The same semi-lunar striations are present on the lips, the same masses of dense cuticle on the outer surface of the lips, the onchia are in the same positions relative to the mandibles (that is, posterior to them) and the mandibles have exactly the same appearance. There is no indication of a distinct bar joining the so-called lateral bars of the mandibles as is illustrated by Wieser (1953) and by Southern (1914).

As a result *Hyalacanthion* must fall as a synonym of *Epacanthion* and I can see no reason to recognize two genera for the species previously grouped in the two genera. I am quite sure that the differences reported in the structure of the mandibles simply reflect the condition of the specimens when they were studied. But if later careful study shows a need for two genera a new name will be required. *Hyalacanthion multipapillatum* Wieser, 1959 is, therefore referred to the genus *Epacanthion* as a new combination.

E. oliffi is distinct from all the species with short spicules in lacking a gubernaculum and a pre-cloacal supplement and in the presence of such a large number of cervical setae. The species most similar to it appears to be *E. multipapillatum* (Wieser, 1959) in which the spicules are short and serrated but this species possesses a gubernaculum and a series of pre-cloacal supplements.

Rhandodemania dura sp. nov.

(Text-figs. 23–25)

Material studied. 11 ♂, 6 ♀, 1 larva. Polluted sediments in the mouth of Durban Harbour, Republic of South Africa (M23n4, collected 20.vi.1964). B.M. (N.H.) Reg. Nos. 1965.994–1003.

	A	B	C	V	Body length (mm.)
Males	32·02	7·01	24·38	—	3·17
	30·38	6·92	20·77	—	3·22
	33·57	6·97	24·19	—	3·29
	36·22	6·93	22·90	—	3·55
Females . . .	34·32	6·37	22·71	54·30	3·02
	34·40	7·51	26·26	57·56	3·44
	32·84	7·09	23·87	53·63	3·58
	40·32	7·01	23·01	54·67	3·75
Larva	35·00	4·93	15·98	—	1·47

Measurements (in mm., in order of body lengths)

Males: Body breadth: 0·099; 0·106; 0·098; 0·098. Oesophagus length: 0·452; 0·465; 0·472; 0·512. Diameter of head: 0·016; 0·018; 0·017; 0·018. Length of cephalic setae (long/short): 0·0084/0·0063; 0·0083/0·0069; 0·0085/

0·0064 ; 0·0087/0·0065. Depth of buccal cavity : 0·020 ; 0·017 ; 0·019 ; 0·018. Length of spicules : 0·055 ; 0·045 ; 0·052 ; 0·048. Length of gubernaculum : 0·029 ; 0·026 ; 0·028 ; 0·031. Length of tail : 0·130 ; 0·155 ; 0·136 ; 0·155. Cloacal diameter : 0·058 ; 0·058 ; 0·057 ; 0·056.

FEMALES : Body breadth : 0·088 ; 0·100 ; 0·109 ; 0·093. Oesophagus length : 0·474 ; 0·458 ; 0·505 ; 0·535. Diameter of head : 0·018 ; 0·016 ; 0·017 ; 0·019. Length of cephalic setae (long/short) : 0·0082/0·0063 ; 0·0085/0·0062 ; 0·0086/0·0061 ; 0·0084/0·0065. Depth of buccal cavity : 0·021 ; 0·022 ; 0·022 ; 0·020. Length of tail : 0·133 ; 0·131 ; 0·150 ; 0·163. Anal diameter : 0·057 ; 0·066 ; 0·065 ; 0·054. Distance of vulva from anterior end of body : 1·64 ; 1·98 ; 1·92 ; 2·05. Size of eggs : 0·045 × 0·165 ; 0·041 × 0·142 ; 0·054 × 0·123 (as examples).

LARVA : Body breadth : 0·042. Oesophagus length : 0·298. Diameter of head : 0·012. Length of cephalic setae (long/short) : 0·0064/0·0037. Depth of buccal cavity : 0·016. Length of tail : 0·092. Anal diameter : 0·028.

The species is typical of the genus with the usual three pairs of long tooth-like structures which represent modified mandibles (see Inglis, 1964) and with the lip region of the head marked by striations (Text-fig. 23). There is a fairly prominent dorsal onchium and no ventro-lateral onchia.

The tail is bluntly rounded with a series of long stout setae, in the male (Text-fig. 25).

The spicules are slim with prominent caps on their proximal ends and are doubled at their distal ends (Text-fig. 24). They are roughly the same width along the whole of their lengths when viewed from the lateral aspect but have a ridge developed on their inner surfaces which can only be easily seen when the specimen being studied is viewed from a slightly ventral aspect. The gubernaculum is relatively long and slim with a very slight expansion towards the proximal end (Text-fig. 24).

Discussion

This species is characterized by the presence of only a dorsal onchium, by the slim shape of the spicules and gubernaculum, and by the cephalic setae being arranged in one circle only. In many ways it is similar to *R. nancyae* Inglis, 1964 which is also from South African waters but the shape of the spicules and gubernaculum is totally different while ventro-lateral onchia are totally lacking, although very reduced in *R. nancyae*.

Family **IRONIDAE**

The next species to be described differs from all others referred to the family in so many characters as to warrant reference to a new genus, thus :

PHERONOUS gen. nov.

Ironidae : cephalic sense organs all papillose ; two dorsal onchia and one on each ventro-lateral sector of the oesophagus ; no caudal glands.

TYPE SPECIES : *Pheronous ogdeni* sp. nov.

PHERONOUS OGDENI gen. et. sp. nov.

(Text-figs. 17–22)

MATERIAL STUDIED. 12 ♂, 16 ♀, 4 larvae. Beach sand in the surf zone. Near Durban, Republic of South Africa (B8n8). B.M. (N.H.) Reg. Nos. 1965.974–993.

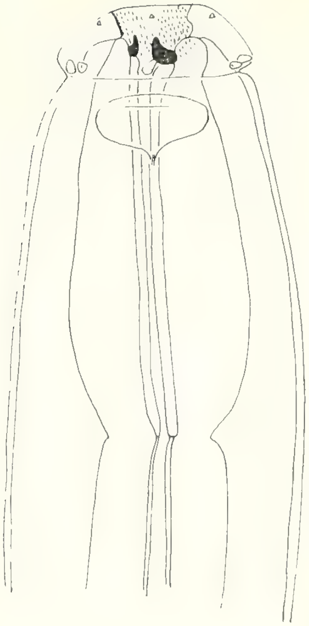
	A	B	C	V	Body length (mm.)
Males	24·03	5·30	22·24	—	1·49
	34·71	5·73	26·03	—	1·77
	33·58	5·39	22·82	—	1·78
	38·83	5·52	25·38	—	1·98
Females . . .	27·50	5·34	14·59	52·45	1·43
	30·85	4·98	14·36	57·93	1·45
	28·81	6·06	13·94	56·58	1·52
	31·45	6·43	16·02	54·76	1·73
	34·04	6·48	15·13	53·67	1·77

MEASUREMENTS (in mm., in order of body lengths)

MALES: Body breadth: 0·062; 0·051; 0·053; 0·051. Oesophagus length: 0·281; 0·309; 0·330; 0·317. Diameter of head: 0·031; 0·023; 0·026; 0·023. Length of pharyngeal rods: 0·056; 0·062; 0·058; 0·057. Distance of nerve ring from anterior end of body: 0·128; 0·147; 0·140; 0·168. Length of spicules: 0·047; 0·041; 0·039; 0·035. Length of gubernaculum: 0·016; 0·019; 0·018; 0·020. Length of tail: 0·033; 0·032; 0·033; 0·033. Cloacal diameter: 0·067; 0·068; 0·076; 0·078.

FEMALES: Body breadth: 0·052; 0·047; 0·054; 0·055; 0·052. Oesophagus length: 0·268; 0·291; 0·251; 0·269; 0·273. Diameter of head: 0·023; 0·019; 0·027; 0·025; 0·024. Length of pharyngeal rods: 0·055; 0·059; 0·057; 0·054; 0·056. Distance of nerve ring from anterior end of body: 0·121; 0·140; 0·123; 0·127; 0·124. Length of tail: 0·098; 0·101; 0·109; 0·093; 0·123. Anal diameter: 0·026; 0·029; 0·032; 0·033; 0·028. Distance of vulva from anterior end of body: 0·75; 0·84; 0·86; 0·93; 0·95.

The head is distinctly set-off from the remainder of the body by a constriction about the level at which the prominent oval shaped amphids open by narrow slits (Text-figs. 17 and 18). The mouth opening is bounded by three lip-lobes and is surrounded by six small papillae. The outer cephalic sense organs form one circle of stout papillae of which six are more prominent than the remaining four (Text-figs. 17, 18 and 19). The buccal cavity is lined by a large number of small wholly cuticular denticles and the anterior end of the oesophagus bears a series of wholly cuticular onchia. There is a pair of small onchia on the dorsal sector of the oesophagus and a single larger onchium on each ventro-lateral sector (Text-fig. 20). The anterior end of the oesophagus is modified as a distinct oesophastomal region in which the



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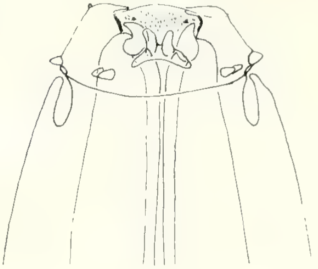

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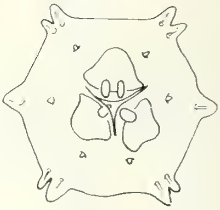

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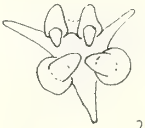

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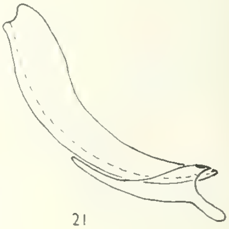

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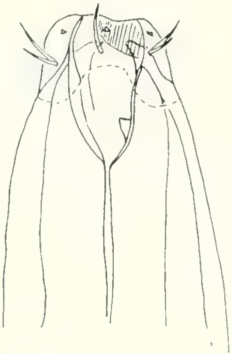

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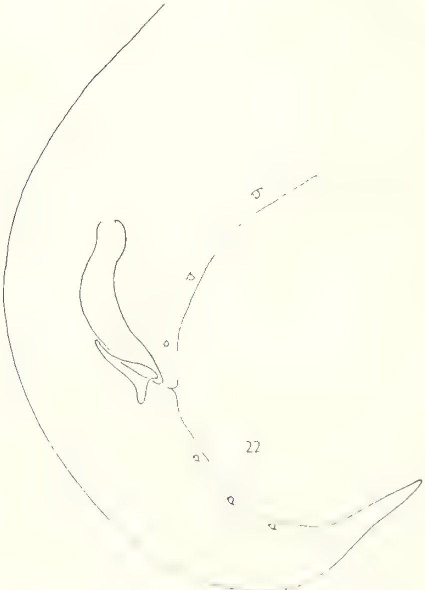

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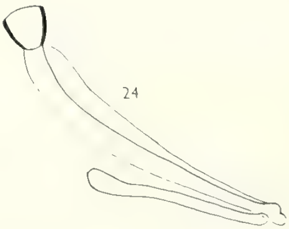

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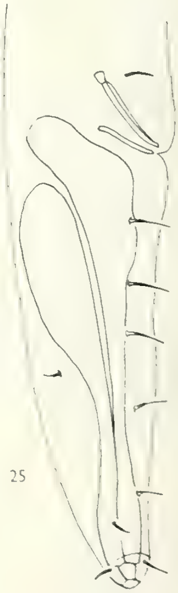

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FIGS. 17–22. *PHERONOUS ogdeni* gen. et sp. nov. Fig. 17. Lateral view of head and oesophastomal region of body. Fig. 18. Dorsal view of head. Note double onchia. Fig. 19. *En face* view of head. Fig. 20. Sketch of onchia *en face*. Fig. 21. Detail of spicule and gubernaculum from the right. Fig. 22. Lateral view of male tail.

FIGS. 23–25. *Rhabdodemania dura* sp. nov. Fig. 23. Lateral view of head with the dorsal surface to the right. Fig. 24. Detail of spicule and gubernaculum from the right. Fig. 25. Lateral view of male tail.

musculature runs slightly anteriorly (Text-fig. 17) and in which the cuticular lining is very prominent. The slim oesophagus expands evenly towards its posterior end.

The tail tapers to a sharp point and there are no caudal glands. In the male the tail bears a series of three pairs of small ventro-lateral papillae and a series of four pairs of similar papillae anterior to the cloacal opening (Text-fig. 22). The spicules are stout and clumsy in appearance without any particularly characteristic features although a dorsal strengthened rib sometimes appears to be present. The gubernaculum is small and enfolds the distal ends of the spicules (Text-fig. 21).

Discussion

This species is unusual in lacking caudal glands, otherwise it would be referable to the genus *Dolicholaimus*. It is possible that it also differs from the species generally referred to that genus in possessing a pair of small dorsal onchia but this is still uncertain (see Inglis, 1961).

Family **ONCHOLAIMIDAE**

Metoncholaimus murphyi sp. nov.

(Text-figs. 26–32)

Material studied. 3 ♂, 1 ♀. Beach sand in surf zone. Near Durban, Republic of South Africa (B8n8). B.M. (N.H.), Reg. Nos. 1965.1012–1015.

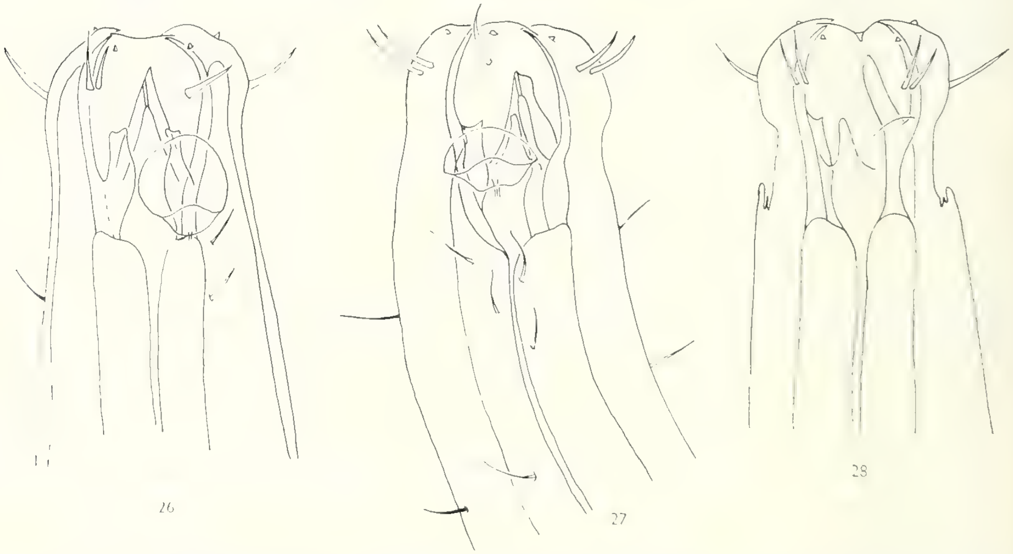
	A	B	C	V	Body length (mm.)
Males	61·05	5·31	62·71	—	2·32
	64·36	5·86	66·05	—	2·51
	61·05	5·31	62·71	—	2·32
Female. . . .	52·31	5·55	59·13	70·22	2·72

Measurements (in mm., in order of body lengths)

Males: Body breadth: 0·038; 0·039; 0·038. Oesophagus length: 0·437; 0·428; 0·419. Diameter of head: 0·027; 0·024; 0·026. Length of cephalic setae (long/short): 0·012/0·008; 0·011/0·009; 0·012/0·008. Buccal cavity (greatest length/greatest width): 0·035/0·017; 0·032/0·018; 0·035/0·019. Distance of nerve ring from anterior end of body: 0·181; 0·179; 0·198. Length of spicules: 0·082; 0·069; 0·077. Length of tail: 0·037; 0·038; 0·043. Cloacal diameter: 0·029; 0·022; 0·026. Lengths of circum-cloacal setae (p/a1/a2/a3): 0·012/0·017/0·013/0·007; 0·013/0·018/0·016/0·008; 0·016/0·021/0·017/0·009 (see Text-fig. 29 for details).

Female: Body breadth: 0·052. Oesophagus length: 0·490. Diameter of head: 0·036. Length of cephalic setae (long/short): 0·012/0·009. Buccal cavity (greatest length/greatest width): 0·044/0·023. Distance of nerve ring from anterior end of body: 0·22. Distance of excretory pore from anterior end of body: 0·026. Length of tail: 0·046. Anal diameter: 0·036. Distance of vulva from anterior end of body: 1·91. Distance of demanian pore anterior to posterior end of body: 0·072. Distance of uvette anterior to posterior end of body: 0·26. Distance of osmosium anterior to uvette: 0·36. Length of uterine efferent: 0·66.

The head is typical with a fairly long buccal cavity with roughly parallel sides (Text-figs. 26, 27 and 28). There is an inner circle of six papillae and an outer circle of cephalic setae of which six are slightly longer than the remaining four. The left ventro-lateral onchium is considerably larger than the smaller and equal dorsal and right ventro-lateral onchia, both of which have somewhat blunt, slightly doubled anterior ends (Text-figs. 26 and 27). The amphids are prominent with slightly different degrees of development of the anterior concavity (Text-figs. 26, 27 and 31).



Figs. 26–28. *Metoncholaimus murphyi* sp. nov., head. Fig. 26. Left-ventro-lateral view. Fig. 27. Wholly lateral view. Fig. 28. Wholly dorsal view.

The male tail is short and sharply curved, almost hook-like, with a pair of long stout post-cloacal setae (p in Text-fig. 29), and two similar pairs flanking the cloacal opening, of which the more posterior is longer than the more anterior (a1, a2 in Text-fig. 29). In addition there is a further pair of shorter setae (a3 in Text-fig. 29) which appear to be slightly longer than the setae occurring on the general body surface except that, while these latter body setae vary somewhat in position from specimen to specimen, this pair (a3) is always found in the same position.

The equal and identical spicules are long and slim and a small gubernaculum may be present (Text-fig. 29) but this is uncertain. There is a marked thickening of the cuticle to form a bump on the body, just anterior to the cloacal opening, into which a duct appears to open. The structure is definitely present but its details could not be established with certainty (Text-figs. 29 and 32).

The female tail is short and stout (Text-fig. 30) and the demanian system empties through a single pore which opens slightly to the left of the mid-ventral line of the body. The details of the demanian system could not be wholly established but (using the terminology of Cobb, 1930) the *uvette* is surrounded by leaf-like elements, the *uterine efferent* is long, stout and easily seen and the *osmosium* could be identified 0·364 mm. anterior to the *uvette*. The relative measurements of the various parts that could be identified are given above.

Discussion

This is a typical member of the genus *Metoncholaimus* which can be easily distinguished by the presence of only one demanian pore in the female (otherwise known only from *M. haplotretos* Mawson, 1958*a*), by the extreme length of the spicules in association with the form of the male tail, by the small number of long circum-cloacal setae, and by the length of the cephalic setae.

WIESONCHOLAIMUS Gen. Nov.

The specimens described below resemble most closely those referred to the genus *Metaparoncholaimus* De Coninck & Schuurmans Stekhoven, 1933 in the unpaired female reproductive system, the two long, equal ventro-lateral onchia and the presence of a demanian system. It differs markedly, however, in the presence of the large gubernaculum, the form of the tail and the long, slim spicules. It is, therefore, referred to a new genus, thus :

WIESONCHOLAIMUS gen. nov.

Oncholaimidae : ventro-lateral onchia equal and larger than dorsal ; tail long and stout. MALE : spicules very long and slim ; large gubernaculum present. FEMALE : Demanian system present.

TYPE SPECIES : *Wiesoncholaimus mawsonae* sp. nov.

WIESONCHOLAIMUS MAWSONAE gen. et sp. nov.

(Text-figs. 33–35)

MATERIAL STUDIED. 6 ♂, 12 ♀. Polluted sediments in the mouth of Durban Harbour, Republic of South Africa (M23n11). B.M. (N.H.) Reg. Nos. 1965.1016–1030. (Holotype selected from this sample.)

2 ♂, 11 ♀, 8 larvae. From same locality on same date at a depth of 40 feet (M23n4). B.M. (N.H.) Reg. Nos. 1965.1031–1040.

	A	B	C	V	Body length (mm.)
Males	70·16	12·14	44·02	—	4·49
	64·93	11·29	41·22	—	4·74
	70·27	12·09	40·94	—	5·20
Females . . .	51·41	9·85	31·96	67·75	4·73
	54·95	10·87	33·84	64·38	5·11
	54·76	13·76	34·81	64·72	5·64

MEASUREMENTS (in mm., in order of body lengths. All ex M23n11)

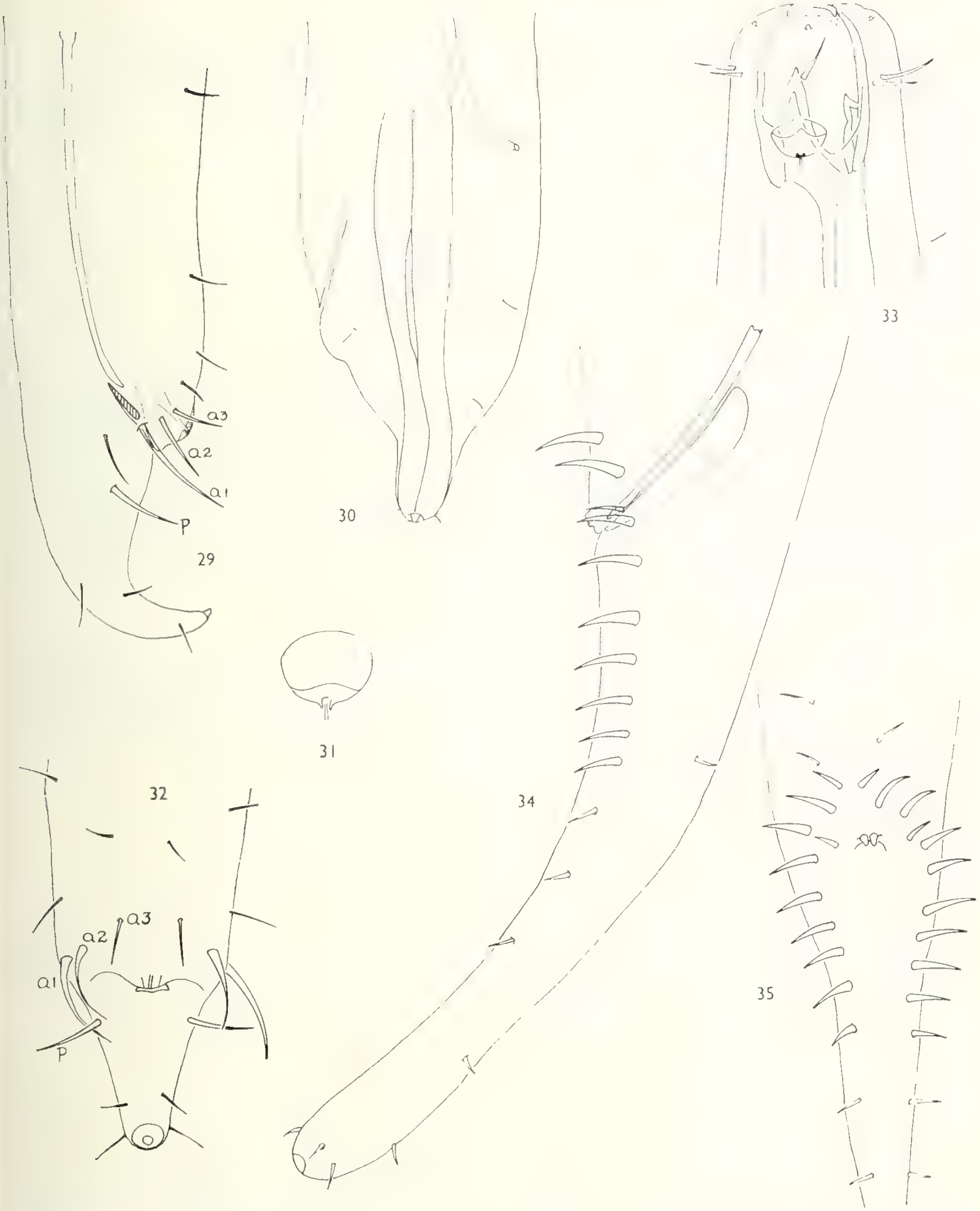
MALES : Body breadth : 0·064 ; 0·073 ; 0·074. Oesophagus length : 0·37 ; 0·42 ; 0·43. Diameter of head : 0·033 ; 0·030 ; 0·030. Length of cephalic setae (long/short) : 0·0090/0·0051 ; 0·0088/0·0053 ; 0·0091/0·0052. Dimensions of buccal cavity (length/breadth) : 0·032/0·018 ; 0·038/0·016 ; 0·033/0·018. Distance of excretory pore from anterior end of body : 0·095 ; 0·103 ; 0·096. Length of spicules : 0·189 ; 0·211 ; 0·183. Length of tail : 0·102 ; 0·115 ; 0·127. Cloacal diameter : 0·032 ; 0·032 ; 0·035.

FEMALES : Body breadth : 0·092 ; 0·093 ; 0·103. Oesophagus length : 0·48 ; 0·47 ; 0·41. Diameter of head : 0·032 ; 0·030 ; 0·030. Length of cephalic setae (long/short) : 0·0086/0·0049 ; 0·0092/0·0051 ; 0·0087/0·0050. Dimensions of buccal cavity (length/breadth) : 0·033/0·020 ; 0·038/0·020 ; 0·035/0·019. Distance of excretory pore from anterior end of body : 0·089 ; 0·121 ; 0·107. Length of tail : 0·148 ; 0·151 ; 0·162. Anal diameter : 0·038 ; 0·040 ; 0·036. Distance of vulva from anterior end of body : 3·11 ; 3·29 ; 3·65. Size of eggs : 0·083 × 0·0067 ; 0·097 × 0·078 ; 0·070 × 0·106 (as examples).

The head bears an inner circle of six papillae surrounding the six-lobed mouth opening and an outer circle of ten setae of which six are longer than the remaining four. The amphids are smallish and lie about the level of the posterior quarter of the buccal cavity. The buccal cavity contains two large, equal ventro-lateral onchia and a smaller dorsal onchium (Text-fig. 33).

The tail is long and stout in both sexes (Text-fig. 34) and in the male the spicules are long, slim and equal in length. The gubernaculum is relatively massive (Text-fig. 34). There is a doubled papilla-like structure on the anterior lip of the cloacal opening in the male (Text-figs. 34 and 35) but no details of any nerves or ducts could be seen. The male tail bears a series of long, stout setae which continue anteriorly to surround the cloacal opening (Text-fig. 34). The number of these setae varies slightly from eight to ten and they are not always wholly symmetrical. Nevertheless there is always a pair of smaller setae flanking the cloacal opening (Text-figs. 34 and 35). In addition there is a variable number of smaller, thorn-like setae on the surface of the tail.

The demanian system is well developed in the females and opens by two dorso-lateral pores which lie 0·23 mm. anterior to the anus in a specimen 4·9 mm. long (from sample M23n4). A most characteristic feature of the system is that the *uvette*,



FIGS. 29–32. *Metoncholaimus murphyi* sp. nov. Fig. 29. Lateral view of male tail. Fig. 30. Lateral view of female tail. Fig. 31. Variant form of amphid. Fig. 32. Ventral view of male tail. (Labelling on Figs. 29 and 32 is defined in the text.)

FIGS. 33–35. *WIESONCHOLAIMUS mawsonae* gen. et sp. nov. Fig. 33. Lateral view of head with dorsal surface to the right. Fig. 34. Lateral view of male tail. Note that for convenience the whole length of the spicule is not drawn. Fig. 35. Ventral view of male tail.

which lies 0·52 mm. anterior to the anus, is a simple spherical organ from which a stout *uterine efferent* runs anteriorly and a thin duct runs posteriorly. This single duct is very easily seen and is a distinct structure as I have established by dissection. It has not, however, been possible to establish any further details of the structure of the demanian system in spite of several attempts.

Discussion

See above, page 97.

Family **LEPTOLAIMIDAE**

PLECTOLAIMUS gen. nov.

This species described below is clearly related to those generally referred to the family Leptolaimidae (sensu de Coninck, 1965) and is most similar to the members of the genera *Chronogaster* Cobb, 1913 and *Halaphanolaimus* Southern, 1914. It differs from them both in the form of the posterior end of the oesophagus and the modification of the anterior end of the oesophagus (in which it is convergent with the Rhabditoid genera *Odontorhabditis* Timm, 1959 and *Cheilorhabditis* Timm, 1959). In addition it appears to differ in the presence of very distinct lips. The genus may be diagnosed thus :

PLECTOLAIMUS gen. nov.

Leptolaimidae : mouth bounded by six distinct lips ; onchia-like structures developed at anterior end of oesophagus from ventro-lateral sectors ; post-oesophageal bulb-like region present with small tri-valvulate structure ; pre-cloacal rod-like supplements present on ventral surface of male.

Type species : *Plectolaimus juliani* sp. nov.

PLECTOLAIMUS JULIANI gen. et sp. nov.

(Text-figs. 36–43)

Material studied. 1 ♂. Beach sand in surf zone. Near Durban, Republic of South Africa (B8n8). B.M. (N.H.) Reg. No. 1965.973.

A	B	C	Body length (mm.)
55·58	20·21	31·76	2·89

Measurements (in mm.)

Body breadth : 0·052. Oesophagus length : 0·143. Body breadth at level of amphids : 0·017. Diameter of amphids : 0·0065. Length of cephalic setae : 0·013. Distance of excretory pore from anterior end of body : 0·058. Length of spicules : 0·062. Length of gubernaculum : 0·018. More posterior pre-cloacal supplement (distance anterior to cloacal opening/length) : 0·059/0·033. More anterior pre-cloacal supplement (distance anterior cloacal opening/length) : 0·124/0·044. Length of tail : 0·091. Cloacal diameter : 0·065.

The cuticle is marked by distinct annules separated from each other by narrow, shallow striations which start at the base of the lips. The annules are marked by distinct elongate punctations over the lateral region of the body from about the middle of the oesophagus to the tip of the tail (Text-fig. 38). There are two files of pores on each lateral surface of the body over its whole length.

The mouth opening is bounded by six very distinct lips each of which bears two papillae (Text-fig. 36). More posteriorly, about the level of the anterior end of the oesophagus, there are four prominent, stout setae. The amphids are circular pits into which the nerves enter on the dorsal side. There is a distinct cheilostome. The anterior end of the oesophagus is modified as an elongate region with thickened walls, at the anterior end of which are two flat onchial-like modifications. These structures are at different levels so that from the ventral view the structure on the left ventro-lateral sector of the oesophagus lies anterior to the corresponding structure on the right ventro-lateral sector. In addition both project dorsally to lie in a pocket formed in the dorsal sector of the oesophagus (Text-figs. 36 and 40).

Posterior to the strongly cuticularized oesophastomal region is a region in which the dorsal sector of the oesophagus develops a slightly rounded bulge which displaces the ventro-lateral sectors. This region does not bear any tooth like structures. Posterior to this region the lumen of the oesophagus develops radial tubes which continue posteriorly for about two-thirds of the length of the oesophagus when they disappear. It has not been possible to make this out in detail but there is definitely no indication of a median bulb.

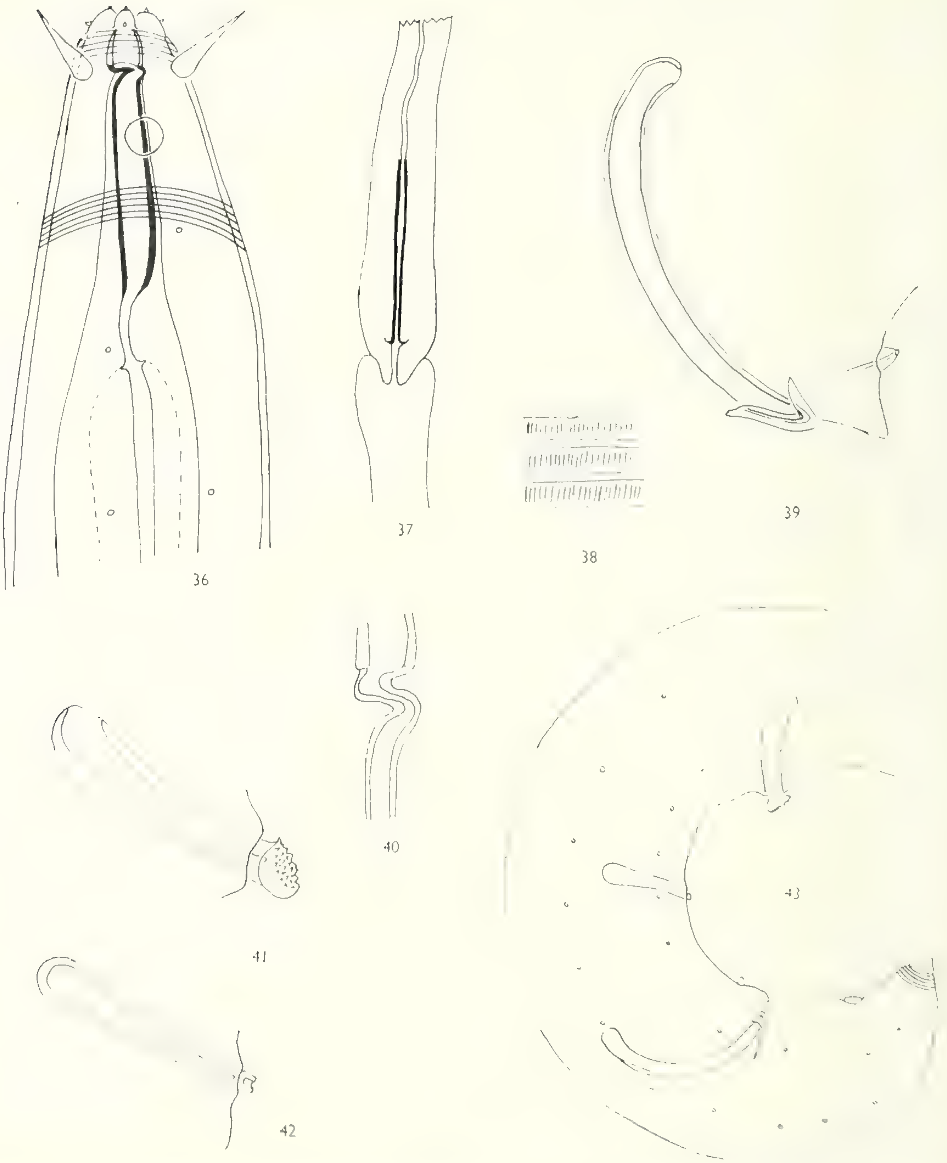
The posterior end of the oesophagus is slightly club shaped and no definite bulb is present. Nevertheless internally it is modified to form a distinct small tri-valvulate structure at the posterior end of a long region in which the cuticular lining of the lumen of the oesophagus is markedly thickened (Text-fig. 37).

The tail is short and stout and is curved strongly ventrally (Text fig. 43) so that the measurements of this region are probably rather low. On the tail roughly half way between the tip and the cloacal opening is a distinct papilla like structure while on the mid-ventral line of the body anterior to the cloacal opening there are three supplementary organs. Of these the most posterior lies just anterior to the cloacal opening and is a prominent papilla-like organ. The details of its structure are uncertain as the body is in a rather poor condition in this region but such a structure is definitely present and a nerve supplies it (Text figs. 39 and 43). The remaining pre-cloacal supplements are more typical. They are long massively cuticularized rods of which the more posterior (Text fig. 42) is rather simple in structure with a slight pit in its distal, protruding end. The more anterior is more massive and the distal end is expanded into a cap covered by many small denticles (Text fig. 41).

The equal and identical spicules are simple in structure being roughly the same width along their full lengths. They terminate distally in slightly rounded tips which are enclosed by a small arrow like gubernaculum (Text fig. 39).

Discussion.

See above, p. 100.



FIGS. 36–43. *PLECTOLAIMUS juliani* gen. et sp. nov. Fig. 36. Anterior end of body from lateral aspect with dorsal surface to the right. Fig. 37. Posterior end of oesophagus. Fig. 38. Sketch showing detail of punctation markings on lateral surface of body. Fig. 39. Lateral view of spicules and gubernaculum. Fig. 40. Sketch of modifications at anterior end of oesophagus from the ventral aspect. Fig. 41. Detail of anterior pre-cloacal supplement. Fig. 42. Detail of posterior pre-cloacal supplement. Fig. 43. Lateral view of male tail.

Family **TRIPYLOIDIDAE**

Bathylaimus deconincki sp. nov.

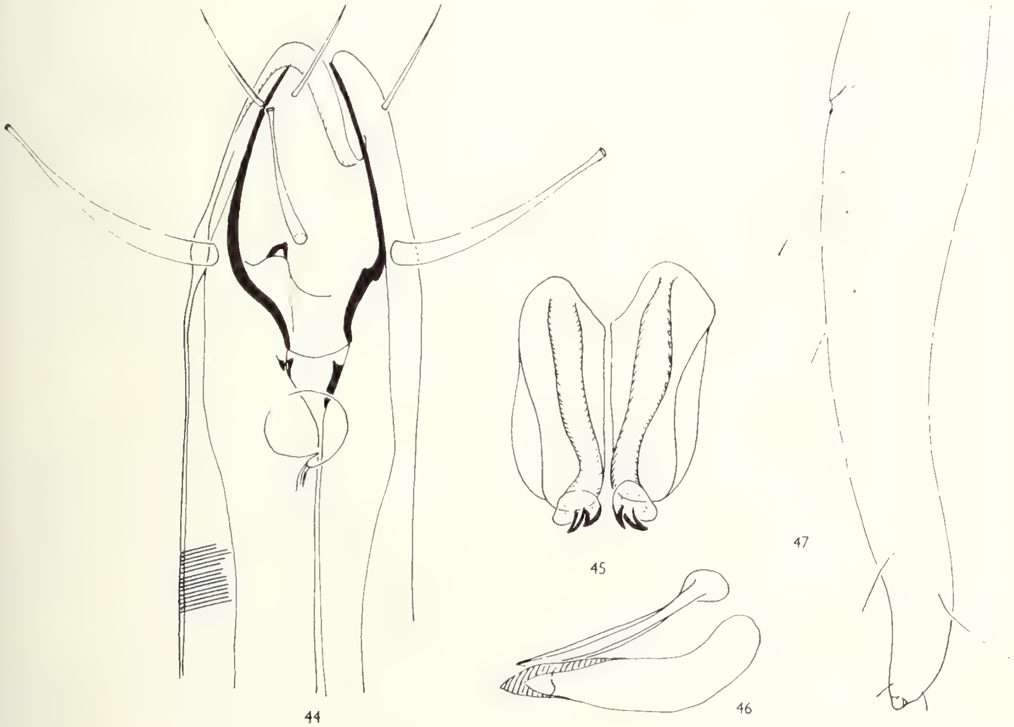
(Text-figs. 44–47)

MATERIAL STUDIED. 1 ♂. Beach sand in surf zone. Near Durban, Republic of South Africa (B8n8). B.M. (N.H.) Reg. No. 1965.994.

A	B	C	Body length (mm.)
57·95	3·48	16·26	2·26

MEASUREMENTS (in mm.)

Body breadth : 0·039. Oesophagus length : 0·65. Diameter of head at level of posterior cephalic setae : 0·030. Diameter of head at level of amphids : 0·034. Lateral diameter of amphid : 0·010. Antero-posterior diameter of amphid : 0·009. Length of more anterior cephalic setae : 0·014. Length of more posterior cephalic setae : 0·038. Depth of buccal cavity from anterior end to level of ventro-lateral onchia : 0·030. Depth of second part of buccal cavity : 0·029. Length of spicules :



FIGS. 44–47. *Bathylaimus deconincki* sp. nov. Fig. 44. Lateral view of head with dorsal surface to the right. Fig. 45. Ventral view of gubernaculum. Fig. 46. Lateral view of spicules and gubernaculum. Fig. 47. Lateral view of male tail.

0·030. Length of gubernaculum: 0·036. Length of tail: 0·139. Cloacal diameter: 0·051.

The cuticle is marked by very fine, close-set transverse striations. The head bears two circles of six setae of which the members of the more posterior circle are typically cup-shaped distally. The four short setae usually associated with this posterior circle were not found but they may have been overlooked. The amphid is a prominent cavity with thin walls into which the nerve enters from the posterior edge (Text fig. 44).

The mouth opening is bounded by three lips which meet at a level roughly half way between the two circles of cephalic setae. The buccal cavity is large and the thick cuticle lining it is continued as a lobe into each lip. In each lip, just anterior to the level at which each lobe of the buccal cavity lining stops, the cuticle is marked by a series of fine antero-posterior striations. The buccal cavity itself is tulip-shaped with two prominent ventro-lateral onchia at the level of its widest part and a slight bump in the corresponding dorsal position. In the region of the oesophagus immediately posterior to the buccal cavity the lumen of the oesophagus is slightly expanded to form a cavity which is not lined by thickened cuticle but which does bear three wholly cuticular onchia (Text-fig. 44). The oesophageal musculature is apparently attached to the cuticle of the body at the level of the more posterior circle of cephalic sense organs.

The tail is fairly stout and carries a series of long, very thin setae which are about 0·02 mm. in length (Text fig. 47). The spicules are short, equal and identical in structure with very distinctly capitate proximal ends and appear to bear very narrow alae. The gubernaculum is the usual massive structure from the lateral aspect with a well chitinized posterior tip and a somewhat slightly chitinized massive region more anteriorly (Text fig. 46). From the ventral aspect, however (Text fig. 45), the gubernaculum is seen to be in two bilaterally symmetrical pieces consisting of a well chitinized median ridge which projects ventrally from a more expanded dorsal plate. The median ridge terminates posteriorly in a swelling from which two tooth-like structures arise on the inner sides (Text-fig. 45).

Discussion

The identification of species referable to this genus is, as with so many others, very difficult in view of the superficiality of most of the available descriptions. It can, however, be said that the genus *Parabathylaimus* De Coninck & Schuurmans Stekhoven, 1933 can certainly be accepted, as Luc & De Coninck (1959) argue, in spite of Wieser's (1956) suggestion that the recognition of a divided or undivided buccal cavity is too difficult to make a useful character.

Delimination of species within this genus appears to be based largely on the use of measurements and the structure of the buccal cavity, in spite of Weiser's comments. Nevertheless the structure of the gubernaculum may be of value but there are very few useful descriptions available. The figures given by de Man (1922) and by De Coninck & Schuurmans Stekhoven (1933) for *B. assimilis* de Man, 1922 suggest that the form of the posterior end of the gubernaculum may be valuable since in that species it is very different from the condition in *B. deconincki*, in that the tooth-like modifications are much longer and slimmer and arise from the outer surface and not the inner as in my species.

This species is otherwise characterized by the posterior position of the large amphid, the form of the tail and, apparently, by the shape and relative lengths of the gubernaculum and spicules.

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STUDIES ON THE BRITISH DERMANYSSIDAE (ACARI : MESOSTIGMATA)

PART II CLASSIFICATION

G. OWEN EVANS
and
W. M. TILL

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 14 No. 5
LONDON : 1966

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By G. OWEN EVANS & W. M. TILL

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SYNOPSIS

The classification of the Dermanyssidae s. lat. is discussed. The free-living, paraphagic, and facultative and obligatory ectoparasitic members of this family in the British fauna are distributed among eight subfamilies (Dermanyssinae, Haemogamasinae, Hirstionyssinae, Laelapinae, Macronyssinae, Melittiphinae, Myonyssinae and Pseudolaelapinae). Keys are given to subfamilies, genera and species. Eighty-one species and subspecies are described and figured.

INTRODUCTION

The earliest suprageneric classification of the mites included in the present study may be attributed to Berlese (1892) who considered them to represent two families, the Dermanyssidae and the Laelapidae. The Dermanyssidae Kolenati, containing the obligatory ectoparasites, included the genera *Ophionyssus* Mégnin, *Leiognathus* Canestrini and *Dermanyssus* Dugès while the free-living forms, paraphages of arthropods and facultative ectoparasites, comprising the genera *Laelaps* Koch, *Hypoaspis* Can., *Seius* Koch, *Iphis* Koch, *Stylochirus* Can., *Neoberlesia* Berl., *Podocinum* Berl. and *Iphiopsis* Berl., were placed in the family Laelapidae Berlese. In his last comprehensive classification of the Mesostigmata published in *Acarotheca Italica* in 1913, Berlese retained his original concepts of the families although, by this time, the large number of new genera added to the Laelapidae in the first decade of this century enabled him to attempt a tribal classification of this family. He proposed four tribes: Laelapini, Iphiopsini (based on Iphiopsidae Kramer), Eviphidini and Phytoseiini.

Subsequent classificatory works on these families have dealt almost exclusively with the "parasitic" forms and the most significant contributions during the thirty years following Berlese's classification are incorporated in the system presented by Vitzthum (1943). This author recognized a single family, Laelapidae, with thirteen subfamilies. The Dermanyssidae sensu Berlese was divided into two subfamilies, Dermanyssinae and Liponyssinae Ewing (= Macronyssidae Oudemans), and the Laelapidae into six subfamilies, namely, Laelapinae, Hypoaspidinae Vitzthum, Hyletastinae Vitzthum (= Eviphidini Berl.), Iphiopsinae, Phytoseiinae and Raillietinae Vitzthum. Three of the remaining five subfamilies, Entonyssinae Ewing, Rhinonyssinae Trouessart and Halarachninae Oudms., contain respectively parasites of the respiratory tract of reptiles, birds and mammals which were included by Berlese (1913) in his family Pteroptidae (= Spinturnicidae Oudms.). Vitzthum further recognized the Haemogamasinae Oudms. and the Podocininae Berl. The subfamilial diagnoses are brief and generalized and, in certain subfamilies such as the Hypoaspidinae and Podocininae, bear little relationship to their generic composition. Nevertheless, Vitzthum's classification provided an excellent summary of the existing knowledge of the group and a basis for subsequent revisionary studies.

Baker & Wharton (1952) modified Vitzthum's classification by distributing his thirteen subfamilies among nine families. Seven of the subfamilies were included in three families and each of the remainder was raised to family status as follows: Laelapidae (Laelapinae, Hypoaspidinae and Hyletastinae), Dermanyssidae (Dermanyssinae and Liponyssinae), Phytoseiidae (Phytoseiinae and Podocininae), Iphiopsidae, Haemogamasidae, Raillietidae, Rhinonyssidae, Entonyssidae and Halarachnidae. No attempt was made to critically examine the classification at generic level.

Evans (1957), in the course of a revision of the British free-living and parasitic members of the Laelapidae sensu Vitzthum, adopted in a restricted sense Baker & Wharton's Phytoseiidae, raised the Eviphidini to family rank and combined the Laelapinae and Hypoaspidinae within the subfamily Laelapinae. Numerous genera previously placed in the Laelapinae, Hypoaspidinae and Podocininae were removed from the complex and distributed among the Aceosejidae and Neoparasitidae. Thus, with the earlier relegation of the Raillietinae into the synonomy (Evans, 1955) and the later elevation of the Podocininae to family status (Evans & Hyatt, 1958) Vitzthum's "Laelapidae" was restricted to the following eight subfamilies: Laelapinae, Iphiopsinae, Haemogamasinae, Dermanyssinae, Macronyssinae, Rhinonyssinae, Entonyssinae and Halarachninae. To these must be added Ixodorhynchinae Ewing (1923), Myonyssinae Bregetova (1956), Histrichonyssinae Keegan *et al.* (1960) and Allolaelapinae Tipton (1960).

This broad concept of the Laelapidae represents one of the two current approaches to the classification of the group. Its protagonists argue that it is premature to attempt a familial classification of the complex when the morphology and biology of a large proportion of its members are so poorly known. Further, new subfamilial categories resulting from piecemeal revisions of the group can be more readily incorporated, provisionally, in a broad family unit than in a more rigid system, the alternative approach favoured by Baker & Wharton. In this latter system certain subfamilies of vertebrate parasites have been withdrawn from the family unit and given familial rank irrespective of their inter-relationships or their relationships with the free-living forms and invertebrate parasites remaining in the Laelapidae. The familial diagnoses are superficial and difficulties arise in the placing of new suprageneric taxa ; for example, the Myonyssinae are included in the Laelapidae by Bregetova (1956) but in the Dermanyssidae by Strandtmann & Wharton (1958). This juggling with subfamilial and familial categories does little to solve the problem of a natural classification of the " Laelapidae ". The basic requirement is a knowledge of the morphology and biology of the group at species level.

The present contribution is restricted to a study of the free-living, paraphagic, and facultative and obligatory ectoparasitic members of the group occurring in the British fauna. In adopting a broad family concept, we have used the oldest available family name, Dermanyssidae Kolenati, 1859. It should be pointed out that this family taxon and the Iphiopsidae Kramer, 1886, have priority over Laelapidae[1] Berlese, 1892.

CLASSIFICATION OF THE BRITISH DERMANYSSIDAE

The adoption of a parasitic mode of life by certain Dermanyssidae realised an evolutionary potential which has produced a vast assemblage of morphologically and biologically diverse forms. Most students of the group consider the parasitic forms to have evolved, in the first instance, from nest-inhabiting laelapines. The transition from a polyphagous free-living to a monophagous parasitic existence probably involved a non-specialized feeding phase that included occasional meals of tissue fluids exuding from skin abrasions of the " host ". Such a generalized type of feeding has been retained by certain species of the genera *Androlaelaps*, *Laelaps* and *Haemogamasus*.

Evans (1955) suggested that the *Hypoaspis* complex may represent the " primitive " free-living group from which this transition was made. Its members show various degrees of association with other animals, either as nest inhabitants or paraphages, a wide range of feeding habits and an extensive geographical distribution. The least specialized members of this complex are probably the predatory forms inhabiting soil and humus, and on the basis of their morphology and ontogenetic development it is possible to define, at least for the purpose of discussion, a basic dermanyssid type with the following characteristics :

Adults : Chelicerae chelate-dentate ; movable digit bidentate in the female, unidentate in the male ; pilus dentilis short, setiform ; dorsal seta and fissures present ; spermadactyl free distally and grooved ; arthrodial processes simple. Gnathosoma with three pairs of hypostomal and

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[1] The genitive stem of *Laelaps* is " Laelap —— " and in accordance with the International Code of Zoological Nomenclature (Articles 29a and 32a (iii)) the family and subfamily taxa become LAELAPIDAE and LAELAPINAE respectively (see Domrow, 1963).

one pair of capitular setae; deutosternum with six transverse rows of denticles; corniculi horn-like, parallel, grooved dorsally to accommodate salivary styli; pedipalps with five free segments and a two-tined apotele, chaetotaxy (2–5–6–14–15); tectum capituli with anterior margin denticulate.

Entire dorsal shield with 39 pairs of setae, of which 22 pairs (*j*1–*j*6, *z*1–*z*6, *s*1–*s*6, *r*2–*r*5) occur in the podonotal region and 17 pairs (*J*1–*J*5, *Z*1–*Z*5, *S*1–*S*5 and *px*2–*px*3) in the opisthonotal region, and 22 pairs of pores. Lateral unsclerotized integument with *r* + *R* series of eight setae and *UR* series.

Tritosternum bipartite, base longer than wide, laciniae pilose. Sternal shield in female with three pairs of setae and two pairs of pores; metasternal setae free. Genital shield flask-shaped with one pair of setae. Anal shield with three setae, euanal setae absent. Opisthogastric cuticle with seven pairs of setae, metapodals small, subcircular. Peritrematal shields free posteriorly, peritreme extending beyond coxa I. Male with holoventral shield bearing ten pairs of setae excluding anals; genital orifice pre-sternal.

All legs six-segmented, excluding pretarsus, and with well developed retractile ambulacra; chaetotaxy as defined for normal condition by Evans & Till (1965), without marked sexual dimorphism.

Larva: Chelicerae chelate, weakly dentate; pilus dentilis simple, dorsal seta and fissures present. Gnathosoma with two pairs of hypostomal setae, capitular setae absent; deutosternum with weakly developed denticles; corniculi horn-like, weak; pedipalps with five free segments and a two-tined apotele, chaetotaxy (0–4–5–12–11); tectum simple.

Podonotal region with ten pairs of setae, nine pairs being situated on a weakly sclerotized podonotal shield; opisthonotum with seven pairs of setae, no pygidial shield.

Tritosternum bipartite, laciniae well developed. Sternal shield with three pairs of setae and two pairs of pores; metasternal and genital setae lacking. Anal shield with three setae, no euanal setae. Opisthogastric cuticle with four pairs of setae. Stigmata, peritremes and associated shields lacking.

Chaetotaxy of legs normal for this instar of the Gamasina (Evans & Till, 1965).

Protonymph: Chelicerae chelate-dentate, movable digit bidentate, pilus dentilis simple, dorsal seta and fissures present. Gnathosoma with three pairs of hypostomal setae, capitular setae present; deutosternum with six transverse rows of denticles, corniculi horn-like; pedipalpal chaetotaxy (1–4–5–12–15). Tectum with weakly denticulate anterior margin.

Podonotal region with 16 pairs of setae, 11 pairs being situated on the podonotal shield. Pygidial shield large, with eight pairs of setae, and the unsclerotized region of the opisthonotum with six pairs. Mesonotal scutellae present.

Tritosternum bipartite. Sternito-genital shield with three pairs of sternal setae and flanked by a pair of genital setae in the region of coxae IV; metasternal setae absent. Anal shield with three setae, euanal setae lacking; opisthogastric cuticle with four pairs of setae. Stigmata present, peritremes short, no peritrematal shield.

Chaetotaxy of legs as defined for free-living Dermanyssidae (Evans & Till, 1965).

Deutonymph: Gnathosoma with characteristics of the female. Dorsal sclerotization comprising single shield with lateral incisions indicating partial fusion of podonotal and opisthonotal elements. Chaetotaxy as in female.

Sternito-genital shield bearing three pairs of sternal setae and one pair of metasternals; genital setae flanking the shield in the region of coxae IV. Metapodal shields subcircular, small. Chaetotaxy of opisthogastric cuticle as in adult. Anal shield with normal three setae, euanals absent. Stigmata with well developed peritremes, peritrematal shields weakly developed. Chaetotaxy of legs as in adult.

Among the *Hypoaspis* complex certain members of the "genera" *Gaeolaelaps* and *Hypoaspis* closely conform to our definition of the basic dermanyssid type, but the group as a whole shows considerable diversity in the external morphology of its post-protonymphal developmental stages, particularly of the female. The general trends in the complex are towards increased sclerotization of the genital shield (*Pseudoparasitus, Ololaelaps, Laelaspis* and *Gymnolaelaps*), hypertrichy of the opisthonotal and opisthogastric regions of the idiosoma of the deutonymph and adults, hypertrichy of tibia III and genu IV and modification of the chelicerae for specialized feeding. In older classifications of the " Laelapidae " considerable emphasis was placed on the size and chaetotaxy of the genital shield at generic and subfamilial levels, but with our knowledge of the morphology of a wider spectrum of the complex it is evident that this character shows considerable variation between congeneric species and does not warrant the taxonomic importance attributed to it by some authors (see Zumpt & Patterson, 1951). Hypertrichy of the idiosoma and legs commonly occurs in those forms showing some degree of association with other animals. It is first evident at the deutonymphal stage and on the dorsal shield is apparent only in the region of the *J* series. Considerable inter- and intrageneric variability is evident in the hypertrichy of the opisthogaster and in the marginal series of the setae (*R* and *UR*). This is very marked in the *Pneumolaelaps* group. Modifications of the chelicerae mainly affect the dentition and the size of the digits, the chelicerae retaining their basic chelate form. In the British representatives of this complex specialization of the chelicerae is found only in certain members of the myrmecophilous group *Laelaspis*. There is no evidence of any marked modification of the hypostome for specialized feeding in the complex and the degree of morphological diversity is of the same order as that found in other families which have radiated into a comparable variety of terrestrial habitats, for example, the Ascidae.

The *Laelaps* complex represents a group of the *Hypoaspis* stock which has evolved in close association with mammals, particularly rodents, and has retained to a remarkable degree the basic morphological features of its free-living, nest-inhabiting progenitors. Members of the genus *Androlaelaps* appear to be the least specialized group of the complex and have a wide geographical distribution in the nests of birds and mammals. Morphologically they can only be separated from species of the *Hypoaspis* complex (*Gaeolaelaps*) by the specialization of the digits and spermadactyl of the male chelicera and, to a lesser extent, by the tendency towards the enlargement of the pilus dentilis in the feeding stages. The functional significance of the non-chelate chelicerae of the males is not known, but this type of chelicera is by no means confined to the *Laelaps* complex. The chelicerae of the males of the myrmecophilous genera *Laelaspis* and *Laelaspulus* approach this condition and essentially similar chelicerae occur in such widely different ecological groups as *Julolaelaps*, associated with millipedes, and *Hemilaelaps*, ectoparasitic on reptiles. As in the *Hypoaspis* complex there is a trend towards increased sclerotization of the genital shield which may bear up to six pairs of opisthogastric setae and in the more specialized members of the complex, *Hyperlaelaps*, *Ondatralaelaps* and *Oryctolaelaps*, hypotrichy of certain palpal segments and of the dorsal shield is not uncommon. Hypertrophy of the leg setae occurs in many species of the complex and these stout, spine-like setae probably assist the movement of the mite through the fur of the host. The *Laelaps* complex appears to be basically polyphagous but with a tendency towards haematophagy in the more specialized members. They are usually considered to be facultative ectoparasites. As the result of the unspecialized type of feeding the gnathosoma shows only minor modifications. Corniculi are present although sometimes reduced in size and degree of sclerotization ; there are five to eight transverse rows of deutosternal denticles with a tendency towards a reduction in the number of denticles in each row ; the labrum is well developed and usually broad and the weakly sclerotized tectum capituli has a smooth anterior margin.

The Haemogamasinae (*Haemogamasus*, *Eulaelaps* and *Brevisterna*) appear to represent another branch of the *Hypoaspis* stock which has evolved in close association with birds and mammals, but show a higher degree of morphological specialization than the *Laelaps* complex. A remarkable feature of the haemogamasines is the extensive hypertrichy of the idiosoma. This is not restricted to the opisthonotum and opisthogaster as in the majority of the *Hypoaspis-Laelaps* group, but extends into the podonotal region and, in some species, to the intercoxal region. Hypertrichy is first apparent at the protonymphal stage and may be restricted to the opisthosoma, as in *Eulaelaps*, or also affect the podonotum, as in *Haemogamasus*. The nature of the sclerotization of the idiosoma in the protonymph, deutonymph and adults of *Eulaelaps* and *Haemogamasus* conforms with the normal *Hypoaspis* type although there is increased sclerotization of the genital and metapodal shields in the female of *Eulaelaps*. In *Brevisterna* reduced sclerotization of the dorsum of the idiosoma is evident and the deutonymph and some adults have an abbreviated dorsal shield and a small discrete pygidial shield. The gnathosoma has been subjected to considerable specialization in the course of the adoption of haematophagy by some species. Invariably the number of transverse rows of deutosternal denticles shows an increase in comparison with the *Hypoaspis-Laelaps* complex and ranges between nine and 16 rows whilst the number of denticles in each transverse row tends to decrease to the extent that the denticles form a single longitudinal file in *Brevisterna*. Typical horn-like corniculi occur in the polyphagous species of *Eulaelaps* and *Haemogamasus* (e.g. *H. pontiger*), but there is a distinct trend towards their modification into membranous flaps in the obligate ectoparasites (*H. liponyssoides, H. hirsutus* and *Brevisterna*). The chelicerae also show considerable diversity in form. Unspecialized feeders retain the typical chelate-dentate form of the free-living *Hypoaspis* type, but in the blood-feeding deutonymphs and females of the group there is a tendency towards a reduction in the dentition of the digits and the enlargement of the pilus dentilis. In the males the chelate form of the chelicerae is retained and the relatively short spermadactyl is never entirely fused with the movable digit. The anterior margin of the tectum may be fimbriated or smooth. The pedipalpal chaetotaxy is normal and the apotele is two- or three-tined. Deviations from the basic *Hypoaspis* type of leg chaetotaxy occur on genu IV and rarely on femora II and III.

Fain (1962), in his detailed study of the Ixodorhynchinae, has pointed out the close affinities of this subfamily with the Laelapinae (*Hypoaspis-Laelaps* group). Its members are ectoparasites of snakes and display some adaptive features which have not been observed in the Laelapinae and Haemogamasinae. The main evolutionary trends are towards decreased sclerotization of the dorsum and, to a lesser extent, the sternal regions of the adults, hypotrichy of the idiosoma and appendages (legs and pedipalps), hypertrichy of the idiosoma, hypertrophy of the coxal setae and corniculi, and the reduction of the fixed digit of the chelicera. The sclerotization of the dorsum of the adults shows considerable diversity and may consist of an entire or laterally incised shield partially covering the idiosoma, or two distinct shields, a podonotal and opisthonotal, which allow greater flexibility of the idiosoma for movement under the scales of the host. Chaetotactic patterns of the idiosoma and segments of the appendages are extremely diverse even among congeneric species. Holotrichy of the dorsum of the idiosoma and of the opisthogaster is rarely, if ever, present, the primary chaetotaxy being reduced by the retardation in the development of certain setae during ontogeny or obscured by regional hypertrichy at the deutonymphal and adult stages. The segmental chaetotaxy of the legs and pedipalps also shows considerable deviation from the normal laelapine type and is apparent in the varying degrees of reduction in the segmental chaetotaxy of the femora, genua and tibiae. Hypertrophy of the postero-ventral setae of coxae I–III and more rarely the antero-ventral seta of coxa I occurs to a greater or lesser degree in all the genera. It is most marked in the genus *Asiatolaelaps* where the postero-ventral seta of coxa I is greatly enlarged and resembles the posterior retrose spur on coxa I in certain ixodid ticks. The corniculi are horn-like and subparallel or convergent in the genera *Hemilaelaps*, *Strandtibbettsia* and *Asiatolaelaps*, but in *Ixodorhynchus* and *Ixobioides* they are greatly enlarged and terminate in one or two retrose hooks which probably serve to anchor the mite to its host in a manner reminiscent of the Metastigmata. The hypostome invariably carries the normal three pairs of setae ; the deutosternum is provided with five to seven transverse rows of denticles (each row comprising one to 20 denticles) and the tectum has a smooth anterior margin. The chelicerae are typically chelate-dentate in the females of *Hemilaelaps* and chelate-edentate in *Asiatolaelaps*. In both genera the pilus dentilis is conspicuous and has a tendency to be enlarged as in the *Laelaps* group. The chelicerae of the females of *Strandtibbettsia*, *Ixodorhynchus* and *Ixobioides* show a reduction in the size of the fixed digit. It is present as a remnant with a pilus dentilis in *Strandtibbettsia* but is completelyl acking in the other two genera. According to Fain (loc. cit.) the chelicerae of the male resemble those of the *Laelaps* group. The nature of the sclerotization of the venter of the idiosoma is surprisingly constant throughout the subfamily ; the sternal shield in the female usually has three pairs of setae and two pairs of pores ; rarely it is reduced in size and carries only two pairs of setae ; the genital shield is typically flask-shaped and bears the genital setae, and the anal shield is large. Stigmata and peritremes are present in both sexes and the peritrematal shield shows various degrees of development. The tritosternum is typically laelapine. The males have a narrow holoventral shield or separate sternito-genital and anal shields. The post-embryonic developmental stages comprise a larva, two active nymphal stages and the adult.

The subfamily Iphiopsinae contains paraphages and parasites of Arthropoda, particularly Insecta and Myriapoda. Little detailed information is available on the morphology and biology of this group and the subfamily at present functions as a depository for the more specialized forms which cannot be accommodated in the subfamily Laelapinae. Our somewhat fragmentary knowledge of the species associated with Myriapoda and Formicidae (Insecta) suggests that the extent of adaptive radiation with its attendant morphological and biological specialization is considerable. The trends in morphological specialization parallel those in members of the family which have evolved in association with vertebrate hosts: reduction in idiosomal sclerotization (*Jacobsonia, Myrmoleichus*), hypertrichy of the idiosoma (*Dinogamasus*), hypotrichy of the idiosoma and the appendages, reduction of the fixed digit of the chelicera (*Berlesia*), elongation and fusion of the spermadactyl with the movable digit of the chelicera in the male (*Julolaelaps*), increase in number of transverse rows of deutosternal denticles (*Myrmonyssus*), reduction in the length of the peritreme and the enlargement of the stigmata (*Iphiopsis*), reduction of claws and the migration of the anus to a terminal position. The hypostome, on the other hand, does not appear to be affected to the same degree as in the vertebrate parasites.

The Myonyssinae probably represent an offshoot of the nest-inhabiting *Hypoaspis-Laelaps* group in which the main evolutionary trend has been towards the specialization of the gnathosoma. This is evident in the shape of the cheliceral shaft, the slender essentially edentate cheliceral digits, the reduction of the pilus dentilis and arthrodial processes, the 9 to 12 rows of deutosternal denticles arranged in a single file and the elongate, distally tapering tectum. On the other hand, the corniculi remain horn-like although often weakly sclerotized. The chaeotaxy of the dorsum of the idiosoma and of the legs and pedipalps is typically laelapine. Varying degrees of hypertrichy of the opisthonotum are present and the genital shield may bear up to 22 setae. The anal shield is characteristically much broader than long. This subfamily contains only the genus *Myonyssus* whose members are facultative (? obligatory) parasites of mammals.

The subfamily Alphalaelapinae is based on the single species *Alphalaelap saplodontiae* (Jellison, 1945), an ectoparasite of the primitive rodent *Aplodontia*. In general appearance the species resembles *Laelaps*, but presents a combination of specialized morphological features which precludes its classification in the Laelapinae. The gnathosoma shows considerable specialization: the deutosternal denticles (up to 14 in number) are arranged in a single file, the corniculi are semi-membranous, the tectum is membranous with a fimbriate anterior margin and the pedipalpal chaetotaxy is (2–4–6–14). Both digits of the chelicerae in the female are modified. The weakly sclerotized fixed digit is slender, tapering distally, and has a hyaline, retrose tooth, but apparently no pilus dentilis, while the movable digit is large, strongly sclerotized, hooked distally and unidentate. In the male the chelicera is of the non-chelate *Laelaps* type with the spermadactyl enormously elongated and about five to six times the length of the cheliceral shaft. The reduced fixed digit lacks a pilus dentilis. Arthrodial processes and dorsal seta are absent. The chaetotaxy of the entire dorsal shield in both sexes is markedly hypotrichous, the podonotal region having 16 pairs of setae (z1 present) and the opisthonotal region 10 pairs (*J*1–5 and *Z*1–5) of which *J*4 and *J*5 are reduced to microsetae. The ventral sclerotization of the female comprises a sternal shield with three pairs of setae and two pairs of pores (the metasternals being free), a large flask-shaped genito-ventral shield bearing six pairs of setae of which two pairs are widely removed from the margins of the shield, and a normal anal shield. A sternito-genito-ventral and discrete anal shield are present in the male. Hypertrichy of the opisthogaster occurs in both sexes and the peritrematal shield is fused with the podal elements of coxa IV. All the legs are strong and terminate in well developed ambulacra. Certain coxal setae are stout and spine-like, and the anterior spine on coxa II is well developed. Coxae III and IV each have a posterior spine as in *Myonyssus*. The chaetotaxy of the leg segments is normal except for tibia II (1—$\frac{2}{1}$, $\frac{2}{1}$—2), genu III (2—$\frac{2}{1}$, $\frac{2}{0}$—1), tibia III (1—$\frac{1}{1}$, $\frac{2}{1}$—1), genu IV (1—$\frac{2}{1}$, $\frac{2}{0}$–1) and tibia IV (1—$\frac{1}{1}$, $\frac{2}{1}$—1). The deutonymph is an active feeding instar with the general characteristics of the female.

The Raillietinae, parasites of the auditory meatus of ungulates, display yet another grade of morphological specialization which is seen in the sclerotization and chaetotaxy of the idiosoma and in the form of the cheliceral digits. Dorsal sclerotization in both sexes is reduced and comprises a relatively small, entire shield reminiscent of the form in some macronyssines. Hypotrichy of the podonotal and opisthonotal regions is very marked in *R. auris* and *R. hopkinsi*, and results from the suppression of a number of setae which normally appear at the protonymphal and deutonymphal instars. The sternal shield in the female is not fused with the podal elements of coxae II and, in the male, the ventral sclerotization consists of a sternito-genital and a discrete anal shield. Both digits of the well sclerotized chelicera are edentate in the female, and the pilus dentilis and dorsal seta are reduced to microsetae or are absent. Well developed arthrodial processes are present at the base of the movable digit. In the male the fixed digit is reduced and the large spermadactyl is fused with the movable digit as in the *Laelaps* group. The hypostome and labrum also resemble those of the *Laelaps* group with the corniculi well sclerotized and blade-like. There are six to eight transverse rows of deutosternal denticles. The pedipalps show a deficiency in tibial chaetotaxy, this segment retaining the larval complement of 12 setae. Deviations from the normal chaetotaxy of the legs occur on femur I (only three ventral setae) and femur III (five setae). The immature stages of the raillietines are not known. Domrow (1961) has provisionally placed within the genus *Raillietia* a species of dermanyssid (*R. australis*) which inhabits the ears of the wombat, *Phascolomis mitchelli* (Owen). This species, of which only the female is known, differs from *auris* and *hopkinsi* in having little or no hypotrichy of the idiosoma and thus shows a closer relationship with the *Laelaps* group.

The subfamilies Dermanyssinae, Macronyssinae, Histrichonyssinae and Hirstionyssinae comprise forms which are obligatory, haematophagous ectoparasites of reptiles, birds and mammals. They exhibit, in varying degrees, the following trends in morphological specialization : reduction in idiosomal sclerotization, hypotrichy of the primary chaetotaxy of the dorsum of the idiosoma, hypertrichy of the lateral and marginal series of dorsal setae and of the opisthogaster, modification of the corniculi and chelicerae, reduction in the number of denticles in each transverse row of deutosternal teeth, enlargement of the antero-dorsal spine of coxa II and diversification of the segmental chaetotaxy of the appendages. These trends are also apparent in many of the other groups of parasitic Dermanyssidae (see above), but it is amongst these subfamilies that we find the most morphologically and biologically specialized ectoparasites of vertebrates. Of the four subfamilies the Hirstionyssinae appear in many ways to be the least specialized. The edentate or weakly dentate form of the chelicerae, the modification of the corniculi into membranous flaps and the single file of deutosternal teeth are adaptive features of the gnathosoma which appear to accompany haematophagy. Some degree of hypotrichy of the dorsal chaetotaxy occurs in all members of the subfamily, but the segmental chaetotaxy of the legs is normal except for deficiencies in the chaetotaxy of tibiae III and IV in some genera. The most significant adaptive trend, however, is towards the development of spur-like structures on the coxae and, to a lesser extent, on the genu and tibia of the anterior pair of legs. These processes, which may be setigerous (hypertrophied setae) or non-setigerous (cuticular protuberances) in origin, undoubtedly assist the mite in its movements through the fur of the host. The life-cycle comprises a non-feeding larva, a (?) feeding protonymph and an active, feeding deutonymph and adult. The genus *Hirstionyssus* and its allies have previously been included in the Macronyssinae, but it is apparent that they represent a bio-morphological group which is quite distinct from the *Macronyssus* complex. Many of the similarities between the two groups in external morphology (gnathosomal features and hypotrichy of the primary setation of the dorsum) are probably the result of convergent or parallel evolution.

Morphological specialization is so advanced in the Dermanyssinae that the external morphology of its members shows little resemblance to that of the laelapine stock. The extreme attenuation of the second cheliceral segment and reduction in the size of the digits in the protonymph, deutonymph and adult female are unique, while the high degree of specialization of the hypostome, the grades of reduction in dorsal idiosomal sclerotization, the hypotrichy of the idiosoma and the diverse segmental chaetotactic patterns of the legs and palps provide little tangible evidence as to the origin of the group or to its relationship with other obligatory ectoparasitic dermanyssids. Within the subfamily the species infesting birds (*Dermanyssus*) display considerably greater morphological plasticity (both inter- and intraspecific), especially as regards chaetotaxy, than do those parasitizing mammals (*Liponyssoides*). The developmental cycle is normal in that it comprises an inactive, non-feeding larva without the cheliceral modifications of the subsequent nymphal stages, an active feeding deutonymph with the general characteristics of the female, and the adult. The protonymph is apparently a more active feeding stage than the equivalent instar in the free-living laelapines.

The Macronyssinae also represent an extremely specialized group of obligatory ectoparasites but, unlike the Dermanyssinae, certain of its members have retained many features of the *Laelaps* group (particularly of *Neolaelaps* and *Notolaelaps*). These features are apparent in *Bewsiella* and *Ichoronyssus*, both parasites of Chiroptera, and may be seen in the general form of the idiosoma and legs, dorsal and ventral sclerotization and slight hypotrichy of the dorsum of the idiosoma and appendages. The occurrence of the more " primitive " macronyssines on Chiroptera has led Radovsky (1964), in his comprehensive and stimulating study of the bat macronyssines, to postulate that the subfamily " has evolved primarily on bats and secondarily to have transferred to other mammals, reptiles and birds ". This seems a logical hypothesis on the basis of the degree of morphological specialization exhibited by the mammal, bird and reptile forms. Certainly, as in the dermanyssines, the parasites of mammals appear to represent the least specialized members of this subfamily, while the forms associated with birds and with reptiles show considerably greater morphological plasticity. All macronyssines have a strongly modified hypostome with hyaline corniculi which, in the majority, form a pre-oral trough. The chelicerae of the protonymph and female are essentially edentate although there is a tendency for the digits of the bat parasites to have denticulate hyaline processes. Only rarely is the fixed digit reduced in the male which has a grooved spermadactyl incompletely fused with the movable digit. Reduction in dorsal idiosomal sclerotization is often marked in both protonymph and female and the dorsal chaetotaxy shows some degree of hypotrichy, the paravertical setae $z1$ rarely being present. Many females and a few protonymphs and males have a conspicuous medio-ventral keel on the trochanter of the pedipalp, a structure which is not known to occur in the Dermanyssinae and is rarely present in the Haemogamasinae (some *Haemogamasus*) and Laelapinae (*Aetholaelaps*). The function of the keels is not known, but they may possibly protect and stabilize the somewhat elongated, membranous hypostome or, as Radovsky (1964) suggests, act as guides for the chelicerae. In addition to the adaptive features of the morphology, the macronyssines display one feature of their biology which is unique amongst the facultative and obligatory ectoparasitic Dermanyssidae, that is, the replacement of the normal, active, feeding deutonymph by a relatively inactive, non-feeding instar which shows considerable degeneration of the feeding organs, tritosternum, idiosomal sclerotization and ambulacra. The presence of this stage (a quasi-calyptostase) has not been established for the genera *Bewsiella* and *Ichoronyssus*. It seems probable that the Dermanyssinae and Macronyssinae represent two distinct bio-morphological groups which have probably evolved quite independently of each other from amongst the Laelapinae.

The Hystrichonyssinae, based on the genus *Hystrichonyssus* whose only known species is an ectoparasite of a Malayan porcupine (*Atherurus macrourus*) and an elephant tree snake (*Acrochordus javanicus*), present yet another combination of adaptive characters which includes modification of the hypostome for haematophagy, extreme elongation of the basal cheliceral segment, reduction in dorsal idiosomal sclerotization and marked hypotrichy of the primary chaetotaxy of the dorsum. Although the chelicerae superficially resemble those of the Dermanyssinae in their extreme length and needle-like proportions, they are the result of a different evolutionary trend, the second segment in *Hystrichonyssus* retaining the typical form of a macronyssine mite. Only the female is known.

The subfamilies Entonyssinae, Rhinonyssinae and Halarachninae contain the endoparasitic members of the Dermanyssidae s. lat. In general, morphological specialization in these groups is characterized by simplification in structure and this is to be seen in the form of the gnathosoma, in the progressive trend towards extreme reduction in idiosomal sclerotization, in the reduction of the tritosternum and in the high degree of hypotrichy of the idiosoma and appendages due to both larval and post-larval specialization. This contrasts with the tendency towards the elaboration of certain structures in the facultative and obligatory parasites, for example, the complex specialization of the hypostome, the hypertrophy of setae to form attachment organs and the hypertrichy of the idiosoma. Each subfamily exhibits grades of morphological specialization and many of the similarities between them are probably the result of convergent or parallel evolution. The least specialized biologically and morphologically are the Entonyssinae which inhabit the respiratory tract of reptiles. They show comparatively little reduction in idiosomal sclerotization and chaetotaxy when compared with the dermanyssids (Ixodorhynchinae) ectoparasitic on reptiles and, in the female, the chelicerae are well developed, chelate-dentate (rarely edentate), and usually have a dorsal seta, arthrodial processes, fissures and a pilus dentilis while in the male the fixed digit is reduced and the long spermadactyl is almost entirely fused with the slender movable digit. All grades of reduction of the tritosternum are evident, from the large bipartite form in *Entonyssus* to its complete absence in *Hamertonia*. The hypostome is simple and weak corniculi may be present or absent. Fusion of the palptibia and tarsus to form a tibiotarsus and a reduction of the apotele occur in some forms. The segmental chaetotaxy of the appendages is diverse. Two active nymphal stages occur in the life-cycle, the deutonymph showing no degeneration of the feeding organs (Fain, 1961). Present morphological and biological evidence suggests that the Entonyssinae have probably evolved from amongst the Ixodorhynchinae. Fain (1961 and 1962) classifies the Ixodorhynchinae within the family Laelapidae but gives familial status to the Entonyssinae. In our opinion this exaggerates the difference between the two groups and has little practical value.

The Rhinonyssinae are parasites of the respiratory tract of birds and the degree of reduction in idiosomal sclerotization and hypotrichy of the idiosoma and appendages exceeds that in the Entonyssinae and in any of the groups of ectoparasitic dermanyssids. Reduction or loss of the tritosternum is a common feature of the group, the peritremes may be strongly reduced or lacking and the stigmata displaced to a dorsolateral position. Modifications of the chelicerae affect the size of the digits, their dentition and shape of the shaft. The gnathosomal and pedipalpal chaetotaxy shows varying degrees of reduction but the hypostome is invariably simple with the corniculi reduced or absent. As in other endoparasitic dermanyssids, the sensory area on tarsus I is extensive with the eupathidia- or solenidia-like setae dispersed and not aggregated as in the free-living and ectoparasitic forms. The life-cycle of the rhinonyssines resembles that of the macronyssines in having an inactive deutonymph with non-functional trophic appendages. Many of the less specialized members of the subfamily, e.g. *Mesonyssoides*, show a striking morphological resemblance to the macronyssines and we are inclined to agree with Radovsky (1964) that the rhinonyssines have probably evolved from the Macronyssinae.

Endoparasites of the respiratory tract of mammals are included in the subfamily Halarachninae. The gnathosoma of the adults is relatively simple ; the hypostome lacks corniculi, the deutosternal denticles are reduced, the pedipalps show a trend towards fusion of the tibia and tarsus and, in *Pneumonyssus*, a marked reduction in the size of the segments, and the apotele may be present or absent. The chelicerae may be small with the digits edentate (*Pneumonyssus*) or strongly developed with the fixed digit reduced or absent in the female (*Halarachne*). Hypotrichy of the venter of the gnathosoma, pedipalps and idiosoma is often very marked. The dorsum is usually partially covered by an entire shield while the genital shield is reduced or absent. Many segments of the legs retain their larval complement of setae. All legs have ambulacra, normally with strong claws. Biologically this group differs from all other known Dermanyssidae in having an extremely active larva which probably functions as the dispersal stage, but no active feeding nymphal stages. The nymphal instar (or instars) described by Hull (1956) for *Pneumonyssus simicola* Banks appears to be non-feeding and of short duration. In *Pneumonyssus* the larval pedipalps show considerably less specialization than in the adult and the legs have long, slender pretarsi with unmodified pulvilli and claws.

Recently Domrow (1961) has described a nymphal (protonymph) dermanyssid from the nasal passages of a marsupial mouse (Dasyuridae) and two species of scale-tailed rats (Muridae). On " purely ecological grounds " this species was placed in the genus *Pneumonyssus* (*Pneumonyssus dentatus* Domrow). The protonymph presents a combination of laelapine and macronyssine characters and is certainly not congeneric with *Pneumonyssus*. In our opinion it should not be classified in the Halarachninae. Macronyssine features are seen in the nature of the sclerotization of the dorsum of the idiosoma which comprises a well defined podonotal shield with the normal eleven pairs of setae, mesonotal scutellae and a reduced pygidial shield bearing seven pairs of setae and similar in form to that of the protonymph of certain *Macronyssus*. The gnathosoma, on the other hand, exhibits certain features of the Laelapinae, horn-like corniculi and up to nine transverse rows of deutosternal denticles, each row being multidentate. The chelicerae are extremely specialized, the basal segment is strongly sclerotized and is about two-thirds the length of the second segment which terminates in a large, hook-like, fixed digit lacking a pilus dentilis while the shorter movable digit is slender and edentate. Hypertrophy of certain gnathosomal and leg setae is also a feature of the species. A decision on the systematic position of *P. dentatus* must await the discovery of the adult stages, but, in the meantime, the unique combination of morphological characters displayed by the protonymph requires recognition and we propose the genus *Domrownyssus* (type : *Pneumonyssus dentatus* Domrow, 1961) for its reception. Provisionally the genus may be placed in the Laelapinae.

The above general review of the characteristics of the major subfamilies of the Dermanyssidae illustrates the high degree of morphological and biological specialization which has accompanied the adoption of a parasitic mode of life by certain members of the family. Each subfamily appears to represent a distinct bio-morphological group and exhibits grades of morphological specialization. A classification of the family purely on the basis of the external morphology of its members is fraught with difficulties, the most significant being the difficulty of defining concise practical units. It is only those groups of obligate ectoparasites, for example the Dermanyssinae and Macronyssinae, in which the transition from polyphagy to monophagy (haematophagy) has been universally accomplished and the accompanying adaptations of the chelicerae, hypostome and life-cycle are more or less stabilized, that a group-diagnosis appears to be at all practicable. In the other groups, the members present grades of morphological specialization depending on the nature of their association with the host. This is clearly seen in the structure of the chelicerae and hypostome of the Haemogamasinae, and in the degree of development of fixation organs (retrograde spurs) in the Ixodorhynchinae. Invariably, the least specialized members of the group provide a link between its more specialized members and the generalized laelapine forms. In these circumstances biological criteria may prove to be of con-considerable value in defining functional suprageneric categories.

The free-living, paraphagic and ectoparasitic members of the Dermanyssidae represented in the British fauna appear to fall, with two exceptions, into six subfamilies or biomorphological groups, namely the Laelapinae, Haemogamasinae, Myonyssinae, Hirstionyssinae, Dermanyssinae and Macronyssinae. The two species which cannot be accommodated in these subfamilies, *Pseudolaelaps doderoi* Berlese and *Melittiphis alvearius* (Berlese), appear to have greater affinities with the Laelapinae than with any other subfamily. We have already referred to the systematic position of *P. doderoi* as being " problematical " (Evans & Till, 1965). This arises from two unusual features of the external morphology of the adults, the marked hypotrichy of the idiosoma and appendages and the trispinate tectum, which immediately distinguish them from any known free-living laelapine. *M. alvearius*, previously classified in the Eviphididae (see p. 273), also presents a combination of morphological characters (form and chaetotaxy of the dorsal shield, sclerotization of the presternal region, nature of the deutosternal denticles etc.) which precludes its classification in the Laelapinae. Provisionally, and as a practical expediency, we are proposing suprageneric categories for each of these species.

The following key to the subfamilies is based on the characteristics of the British species of free-living and ectoparasitic Dermanyssidae. A comprehensive diagnosis of these groups is given elsewhere in the text. It is rarely that any one " character " is sufficiently stable thoughout a subfamily to be entirely diagnostic, therefore the separation of the groups has been based on combinations of characters.

KEY TO THE SUBFAMILIES OF THE BRITISH DERMANYSSIDAE

1 Chelicerae in the nymphal stages and female with the second segment enormously elongated, stylet-like ; digits minute. Males with fixed digit reduced and the elongate spermadactyl entirely fused with the movable digit ; chelicerae never chelate. Tarsi III and IV of the male with seta pv_2 modified into a short, tooth-like projection. Both sexes with paravertical setae absent. Obligatory ectoparasites of birds . . . . DERMANYSSINAE (p. 346)

– Second segment of the chelicerae in nymphal stages and female never conspicuously elongated, digits prominent. Seta pv_2 on the tarsi of the males never modified into a tooth-like projection 2

2 Dorsal shield in deutonymphal and adult stages markedly hypertrichous, setation often resembling a pelage. Genital shield, and sometimes sternal and anal shields, with unpaired accessory setae. Deutosternum with 10 or more transverse rows of denticles, majority of rows compound. Tectum with margins conspicuously

fimbriated. Pedipalpal chaetotaxy normal. Chelicerae normally chelate-dentate in both sexes, rarely edentate, but pilus dentilis prominent. Associated with birds and mammals as nest inhabitants or ectoparasites . HAEMOGAMASINAE (p. 238)

– Hypertrichy of the dorsal shield, when present, restricted to the region of the *J* series or, if more extensive, deutosternal denticles in a single file and no accessory setae on the genital shield 3

3 Genu and tibia I with two ventral setae $(2\text{—}\frac{3}{1},\ \frac{3}{1}\text{—}2)$, genu II with one ventral seta $(2\text{—}\frac{3}{0},\ \frac{2}{1}\text{—}2)$. Tectum trispinate. Marked hypotrichy of the dorsal shield, podonotal region with 15 pairs (paraverticals absent) and opisthonotal with nine pairs of setae. Podal-peritrematal shields in female greatly enlarged posterior to coxae IV and flanking the genito-ventral shield. Chelicerae in both sexes chelate-dentate. Free-living. . . . . PSEUDOLAELAPINAE (p. 265)

– Genu and tibia I normally with three ventral setae $(2\text{—}\frac{3}{2},\ \frac{3}{1}\text{—}2)$,[2] genu II with two ventral setae $(2\text{—}\frac{3}{1},\ \frac{2}{1}\text{—}2)$. Without the above combination of characters . . 4

4 Anal shield in the female considerably wider than long, anterior margin concave (Text-fig. 64B). Chelicerae essentially edentate, digits long and slender in both sexes, spermadactyl entirely fused with movable digit in the male ; pilus dentilis, arthrodial processes and dorsal seta apparently absent. Deutosternum with 9–12 denticles arranged in a single file. Paravertical setae (*z*1) present in both sexes. Genital shield in the female with unpaired accessory setae. Anterior spine of coxa II prominent. Associated with small mammals. . . MYONYSSINAE (p. 268)

– Without the above combination of characters 5

5 Corniculi horn-like, strongly or weakly sclerotized, never in the form of hyaline lobes. Chelicerae in the female usually chelate-dentate, rarely edentate but pilus dentilis present. Chelicerae of the male chelate-dentate with free spermadactyl, or with reduced fixed digit and elongate spermadactyl partially or completely fused with movable digit, non-chelate. Dorsal chaetotaxy holotrichous or hypertrichous, if hypotrichous, paravertical setae present or chelicerae in both sexes chelate-dentate (*Ololaelaps sellnicki*). Free-living, nest inhabitants and facultative (? obligatory) ectoparasites of vertebrates 6

– Corniculi never horn-like, usually in the form of hyaline lobes. Chelicera in the female with digits essentially edentate, often with smooth or denticulate hyaline lobes, pilus dentilis absent. Chelicerae of the male edentate, digits subequal, fixed digits never markedly reduced in length, spermadactyl free distally, rarely approaching the length of the second cheliceral segment. Primary dorsal chaetotaxy invariably hypotrichous, paravertical setae absent. Obligatory ectoparasites of vertebrates. 7

6 Presternal area in the female with a keel-like ridge. Deutosternum in both sexes with about eight denticles arranged in a single file. Cheliceral digits in the female chelate, weakly dentate, pilus dentilis prominent, in the male non-chelate, fixed digit reduced, elongate spermadactyl completely fused with movable digit. Dorsal shield with general hypertrichy. Anal shield (female) or ventro-anal shield (male) with posteriorly directed spur anterior to the anus. Male with sternito-genital and ventro-anal shields. In bee-hives . MELITTIPHINAE (p. 273)

– Presternal area in the female reticulated or with pre-endopodal shields, never with a keel-like ridge. Deutosternum with five to seven (usually six) transverse rows of denticles, rows usually compound, sometimes reduced to a single denticle. Chelicerae in the female chelate-dentate or, rarely, chelate-edentate, pilus dentilis present, in the male chelate-dentate with spermadactyl free anteriorly or non-chelate with edentate fixed digit reduced and spermadactyl entirely or partially fused with the movable digit. Hypertrichy of the dorsal shield, when present, usually restricted to the region of the *J* series of setae. Anal shield never with posteriorly directed spur. Male with holoventral shield or with discrete sternito-genito-ventral and anal shields . . . . LAELAPINAE (p. 124)

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[2] *Ornithonyssus sylviarum* is exceptional in having only two ventral setae on tibia and genu I in some specimens, but the chaetotaxy of genu II is normal $(2\text{—}\frac{3}{1},\ \frac{3}{1}\text{—}2)$.

7 Both sexes with one or more of the coxae with retrograde non-setigerous spurs, excluding the anterior spine of coxa II ; genu IV with one ventral seta. Palptrochanter without medio-ventral keel. Dorsal shield entire in both sexes. Deutonymph active, feeding, and resembling the female in the structure of the gnathosoma and its well developed, bipartite tritosternum HIRSTIONYSSINAE (p. 276)

– Both sexes without retrograde non-setigerous spurs on the coxae (excluding anterior spine on coxa II), at the most with weak ridges ; genu IV with two ventral setae. Dorsal shield entire in the male but with entire, two subequal shields or with discrete podonotal, mesonotal and pygidial elements in the female. Palptrochanter usually with a medio-ventral keel in the female (weakly developed in *Ophionyssus* and some *Ornithonyssus*). Deutonymph inactive, non-feeding, with degenerate (larviform) chelicerae and a simple tritosternum bipartite only at the tip . . . . MACRONYSSINAE (p. 300)

The measurements given in the descriptions of species apply, in most cases, to a single specimen ; no attempt has been made to assess intraspecific variation. They have been taken as follows, unless otherwise stated in the text :

Chelicera : segment I, maximum length ; segment II, from base of segment to apex of fixed digit; movable digit, maximum length; spermadactyl, from base of movable digit to tip of spermadactyl.

Dorsal (*or podonotal*) *shield* : length in midline ; width at level of seta *z*6.

Opisthonotal shield : width at level of seta *J*1.

Pygidial shield : width at level of antero-lateral corners.

Tritosternum : base, to point of division into two laciniae ; laciniae, from point of division to tip.

Sternal shield : length in midline ; width at level of second pair of sternal setae (*st*2).

Genital (*or genito-ventral*) *shield* : length from level of genital setae to posterior margin ; width at level of genital setae (*gen.*).

Anal shield : length in midline to base of postanal seta ; width through middle of anus.

Holoventral shield : length in midline from anterior margin of genital orifice to base of postanal setae ; width at level of second pair of sternal setae (*st*2).

Distances between setae (*st*1, *st*3, *c.s.*, *hyp.* 2, *Jv*2) : from centre of setal bases.

Segments of appendages (*legs and pedipalps*) : median dorsal length ; width at base of segment.

Subfamily **LAELAPINAE** Berlese

Laelaptidae Berlese, 1892, *Acari, Myr. Scorp, Ital.* Ordo Mesostigmata : 30.

Adults : Chelicerae chelate-dentate in the female, movable digit bidentate ; digits rarely edentate. Male chelicera chelate-dentate with spermadactyl long, grooved and free distally or non-chelate with spermadactyl partially or entirely fused with the movable digit ; digits subequal in length or fixed digit markedly reduced, edentate. Pilus dentilis present, setiform or inflated; dorsal seta, fissures and arthrodial processes usually well developed. Chaetotaxy of venter of gnathosoma normal. Pedipalps with five free segments, apotele two- or three-tined, chaetotaxy of trochanter to tibia (2–5–6–14), rarely femur, genu or tibia unideficient (2–5–5–14 ; 2–4/5–6 13/14). Palptrochanter rarely with a medio-ventral spur-like ridge. Deutosternum with five to seven, usually six, transverse rows of denticles; transverse rows sometimes reduced to a single denticle. Corniculi essentially horn-like, rarely with a hyaline expansion. Internal malae simple or branched, margin smooth or fringed. Tectum capituli well sclerotized with anterior margin denticulate, or membranous with smooth anterior margin.

Dorsal sclerotization in both sexes comprising an entire dorsal shield, rarely retaining the deutonymphal incisions. Primary chaetotaxy of dorsal shield comprising 39 pairs of setae of which 22 pairs occur in the podonotal region and 17 pairs in the opisthonotal. Variants are due to addition of one pair of posterior accessories (*px*1), or a pair of anterior accessories (*ax*), or to suppression of posterior accessories (*px* series), *j*3, *z*3, *J*3, *J*4 and *Z*3 and rarely *z*1. Hypertrichy of the shield usually restricted to the region of the *J* series, rarely affecting the entire shield. Marginal series showing considerable diversity in the number of setae. Dorsal setae simple, pilose, subspinose, clavate or cuneiform.

Tritosternum bipartite, laciniae well developed, smooth or pilose. Pre-endopodal shields present or absent. Sternal shield in the female with three, rarely four, pairs of setae and two or three pairs of pores. Metasternal setae, when free, situated on unsclerotized cuticle or on platelets. Genital shield narrow or variously inflated and bearing the genital setae and, in some forms, up to five pairs of opisthogastric setae. Anal shield free or fused with the genito-ventral shield to form a genito-ventro-anal shield (*Ololaelaps*) ; with the normal three setae, no euanal setae ; aciculated area conspicuous. Opisthogastric cuticle with varying grades of hypertrichy. Metapodal shields usually small, rarely fused with the genito-ventral shield. Peritrematal shields usually free posteriorly, but may be fused with the podal elements behind coxae IV. Podal shields poorly or well developed. Stigmata with well developed peritremes usually extending up to or beyond coxa I. Male with holoventral shield, rarely with sternito-genito-ventral and anal shields. Genital orifice presternal.

All legs six-segmented with ambulacra ; claws sometimes reduced or absent. Variants from normal segmental chaetotactic patterns may occur on tibia I ($2—\frac{3}{2}, \frac{3}{2}—2$), genu III ($2—\frac{2}{1}, \frac{2}{1}—2$; $2—\frac{2}{1}, \frac{2}{0}—1$), tibia III ($2—\frac{1}{1}, \frac{2}{1}—2$; $1—\frac{1}{1}, \frac{2}{1}—1$) and genu IV ($2—\frac{2}{1}, \frac{3}{0}—2$; $2—\frac{2}{1}, \frac{3}{1}—2$; $1—\frac{2}{1}, \frac{3}{0}—1$). Anterior spine on coxa II prominent, small, or absent. Seta av_1 on femur II may be modified to form a stout spine or spur in both sexes or in the male only.

Larva : Relatively inactive, non-feeding instar. Chelicerae small, chelate, dentate or edentate ; dorsal setae and fissures present ; pilus dentilis present but often reduced ; arthrodial processes weakly developed or absent. Hypostome with two pairs of setae ; corniculi small, horn-like ; internal malae simple. Deutosternum with five to seven transverse rows of denticles. Pedipalps with five free segments, apotele two- or three-tined, chaetotaxy (0–4–5–12). Dorsal sclerotization weak or absent, podonotal region with ten, rarely nine, pairs of setae. Chaetotaxy of opisthonotum variable. Tritosternum bipartite, laciniae usually smooth. Sternal region with three pairs of setae ; opisthogaster with four pairs, excluding the three setae associated with the anus. Stigmata and peritremes absent. Segmental chaetotaxy of the legs normal for this instar.

Protonymph : Active (?) feeding stage. Gnathosoma, excluding pedipalps, similar to that of the female but not so well developed. Pedipalps with normal chaetotaxy (1–4–5–12).

Dorsal sclerotization comprising well developed podonotal, mesonotal and pygidial elements. Holotrichous condition of the dorsum consisting of 30 pairs of setae ; podonotal shield usually with 10 or 11 pairs, pygidial shield with eight pairs. Tritosternum as in adult. Sternal shield with three pairs of setae and two pairs of pores ; genital setae free on integument. Anal shield normal. Opisthogastric cuticle with four pairs of setae. Stigmata and short peritremes present. Chaetotaxy of legs normal for this instar.

Deutonymph : Active feeding stage. Gnathosoma as in female. Dorsum with a single, incised, rarely entire, dorsal shield. Dorsal chaetotaxy as in adult. Sexual dimorphism affecting marginal series in some forms. Tritosternum as in adult, sternito-genital shield with four pairs of setae (metasternals present) and three pairs of pores ; genital setae free on integument. Anal shield normal. Opisthogastric cuticle with seven pairs of setae or displaying hypertrichy. Peritremes as in adult, peritrematal shield always free posteriorly. Metapodal shields present. Segmental chaetotaxy of legs as in corresponding adult.

KEY TO THE GENERA OF THE BRITISH LAELAPINAE

1 Female with anal shield completely fused with genito-ventral shield. Metasternal setae situated on sternal shield. Dorsal shield arched, completely covering dorsum of mite. Apotele with three unequal prongs . . . ***OLOLAELAPS*** (p. 228)

– Female with anal shield free. Metasternal setae not on sternal shield . . . 2

2 Genu IV with two postero-lateral setae, pl_2 present (2—$\frac{2}{1}$, $\frac{3}{0}$—2). Pilus dentilis long, slender or inflated. Chelicerae of male strongly modified, never chelate . . 3

– Genu IV with one postero-lateral seta (2—$\frac{2}{1}$, $\frac{3}{0}$—1) or, if two postero-lateral setae present, pilus dentilis short, setiform. Chelicerae of male chelate-dentate . . 6

3 Female with genital shield bearing the genital setae only . ***ANDROLAELAPS*** (p. 150)

– Female with genito-ventral shield bearing three pairs of opisthogastric setae in addition to the genitals. 4

4 Medio-dorsal series of setae hypotrichous, *j*3, *J*3, *J*4 lacking. Femur I with seta pd_1 arising from a strong, sclerotized protuberance. Associated with *Ondatra*, introduced . . . . ***ONDATRALAELAPS*** (p. 145)

– Medio-dorsal series of setae normal, comprising 11 pairs of setae (*j*1–*j*6 ; *J*1–*J*5). Seta pd_1 on femur I not arising from a strong protuberance 5

5 Genu III with nine setae. Dorsal setae rarely short, subspinose ; *px*2 and *px*3 present. Male with holoventral shield . . . . ***LAELAPS*** (p. 127)

– Genu III with eight setae. Dorsal setae short, subspinose, never more than one pair of *px* setae. Male with sternito-genito-ventral and anal shields ***HYPERLAELAPS*** (p. 140)

6 Female with large genito-ventral shield bearing four or more pairs of setae of which two pairs are widely removed from its lateral margins. Pedipalpal apotele three-tined, posterior tine small . . . . . . **PSEUDOPARASITUS** (p. 224)

– Female with genital shield bearing genital setae only or, if with genito-ventral shield, the additional setae are situated on its lateral margins. Pedipalpal apotele normally two-tined, rarely with three subequal tines **HYPOASPIS** s. lat. (p. 158)

Genus **LAELAPS** Koch

Laelaps Koch, 1836, *Deutschl. C.M.A.* **4** : 19 ; Koch 1843, *Arachnidensystems* **3** : 88.
Echinolaelaps Ewing, 1929, *Manual of External Parasites* : 10 and 185.
Macrolaelaps Ewing, 1929, *Manual of External Parasites* : 185.
Myolaelaps Lange, 1955, *Opred. Faune SSSR.* **59** : 328.
Rattilaelaps Lange, 1955, *Opred. Faune SSSR.* **59** : 328.
Microtilaelaps Lange, 1955, *Opred. Faune SSSR.* **59** : 329.

Type : *Laelaps hilaris* Koch, 1836.

Medium sclerotized mites ranging from 500 μ to 1,500 μ in length. Chelicerae chelate-dentate in the female with the movable digit bidentate. Fixed digit in the male markedly reduced, normally edentate ; movable digit edentate and partially or entirely fused with the elongated, grooved spermadactyl. Pilus dentilis in both sexes normally large and inflated distally. Dorsal seta and fissures normal. Arthrodial processes present at base of movable digit. Chaetotaxy of venter of gnathosoma and pedipalps normal, apotele two-tined. Deutosternum normally with six, rarely seven, rows of denticles, each row with one to three denticles. Corniculi horn-like, weak to medium sclerotization. Internal malae simple or fringed. Labrum broad, striated. Tectum capituli membranous, rounded anteriorly, never denticulate.

Dorsum of idiosoma with entire shield bearing 39 pairs of setae ; no unpaired accessory setae.

Tritosternum normal, bipartite. No definite pre-endopodal shields. Sternal shield in the female with three pairs of setae and two pairs of pores. Genito-ventral shield variously inflated and bearing four pairs of setae. Pear-shaped anal shield with normal chaetotaxy, paranal setae in line with posterior margin of anus or posterior to it. Opisthogastric cuticle with variable number of setae and affected by sexual dimorphism which is first apparent at the deutonymphal stage. Peritrematal shields free posteriorly, often weakly developed. Metapodal shields present. Male with holoventral shield not fused with peritrematal shields and bearing nine or ten pairs of setae excluding the anals. Podal shields poorly developed posterior to coxae IV.

Chaetotaxy of legs normal except for genu IV which has two postero-laterals $(2\text{—}\frac{2}{1}, \frac{3}{0}\text{—}2)$ and sometimes two ventrals $(2\text{—}\frac{2}{1}, \frac{3}{1}\text{—}2)$. Setae ad_1 and pd_1 on femur I and less conspicuously on femur II enlarged and elongated. Coxal setae often thickened to form stout spine-like structures. Coxa II with anterior spine. Ambulacra of legs II–IV with paired claws. Claws of leg I often reduced.

KEY TO FEMALES

1 Genu IV with two ventral setae (*pv* present) ; paranal setae short, their length equal approximately to width of anus (Text-fig. 1B) . . . ***L. agilis*** Koch (p. 132)

– Genu IV with one ventral seta (*pv* absent) ; paranal setae relatively long, their length at least twice the width of the anus 2

2 Genito-ventral shield greatly expanded behind coxae IV, with posterior margin deeply concave ; distance between genital setae (*gen.*) less than that between *Jv*2. Dorsal setae relatively long ; length of *j*5 distinctly greater than distance between *j*5 and *s*5 (Text-fig. 3A). Pilus dentilis setiform . . **L. echidnina** Berlese (p. 134)

– Genito-ventral shield only moderately expanded behind coxae IV, posterior margin rounded or very slightly concave ; distance between genital setae (*gen.*) greater than distance between *Jv*2. Dorsal setae relatively short ; length of *j*5 distinctly less than distance between *j*5 and *s*5. Pilus dentilis inflated 3

3 Sternal setae relatively long and slender, *st*1 reaching posterior margin of sternal shield. Dorsal setae slender ; marginal opisthogastric setae with bifid tips
L. hilaris Koch[3] (p. 128)

– Sternal setae short and stout, *st*1 reaching base of *st*2. Dorsal setae stout and spine-like ; marginal opisthogastric setae simple . . **L. muris** (Ljungh) (p. 137)

KEY TO MALES

1 Genu IV with two ventral setae (*pv* present) ; tarsus IV with setae ad_2 and ad_3 very long, thick, sword-like, their length at least twice the basal width of the tarsus (Text-fig. 2C). Peritremes relatively short, extending to posterior margin of coxae II. Paranal setae short, their length approximately equal to width of anus. Chelicera as in Text-fig. 2E . . . . **L. agilis** Koch (p. 132)

– Genu IV with one ventral seta (*pv* absent) ; tarsus IV with setae ad_2 and ad_3 setiform or blade-like but not exceeding 1½ times the width of the tarsus. Peritremes longer, extending at least to anterior margin of coxa II. Paranal setae longer, their length at least 1½ times the width of the anus 2

2 Holoventral shield with five pairs of stout setae in genito-ventral region (Text-fig. 5D). Tarsus IV with setae ad_2 and ad_3 blade-like ; seta pv_2 short, stout and spine-like (Text-fig. 5F). Chelicera as in Text-fig. 5B . . · **L. muris** (Ljungh) (p. 139)

– Holoventral shield with six pairs of relatively slender setae in the genito-ventral region. Tarsus IV with setae ad_2 ad_3 and pv_2 normal 3

3 Coxa III with posterior seta stout, spine-like ; tarsus IV with setae al_1 and pv_1 stout and spine-like. Pilus dentilis inflated near its distal end ; chelicera as in Text-fig. 2B
L. hilaris Koch[3] (p. 130)

– Coxa III with posterior seta normal ; tarsus IV with setae al_1 and pv_1 slender, pointed. Pilus dentilis setiform ; chelicera as in Text-fig. 3E
L. echidnina Berlese (p. 136)

Laelaps hilaris Koch

Laelaps hilaris Koch, 1836, *Deutschl. C.M.A.* **4** : 20. Tipton, 1960, *Univ. Calif. Publ. Ent.* **16** : 271, figs.

Female : Chelicera with segment I, 54 μ ; II, 110 μ ; movable digit 33 μ, bidentate ; fixed digit unidentate ; pilus dentilis elongate with swollen tip. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart ; *hyp.* 2 about 54 μ apart. Deutosternum with six transverse rows of denticles (1–2 per row) ; corniculi 27 μ long ; internal

[3] *Laelaps clethrionomydis* Lange (see Bregetova, 1956) commonly occurs on the bank vole, *Clethrionomys glareolus* (Schreber) in Europe and may possibly parastize this host in Britain. It is closely related to *L. hilaris* but may be distinguished from it by the larger number of shorter, more spinose setae of the opisthogaster of the female and by tarsus IV of the male having seta pv_2 short and spine-like and setae $ad_{2\ 3}$ and pd_{2-3} long and blade-like. These tarsal setae are simple, setiform in the male of *L. hilaris*.

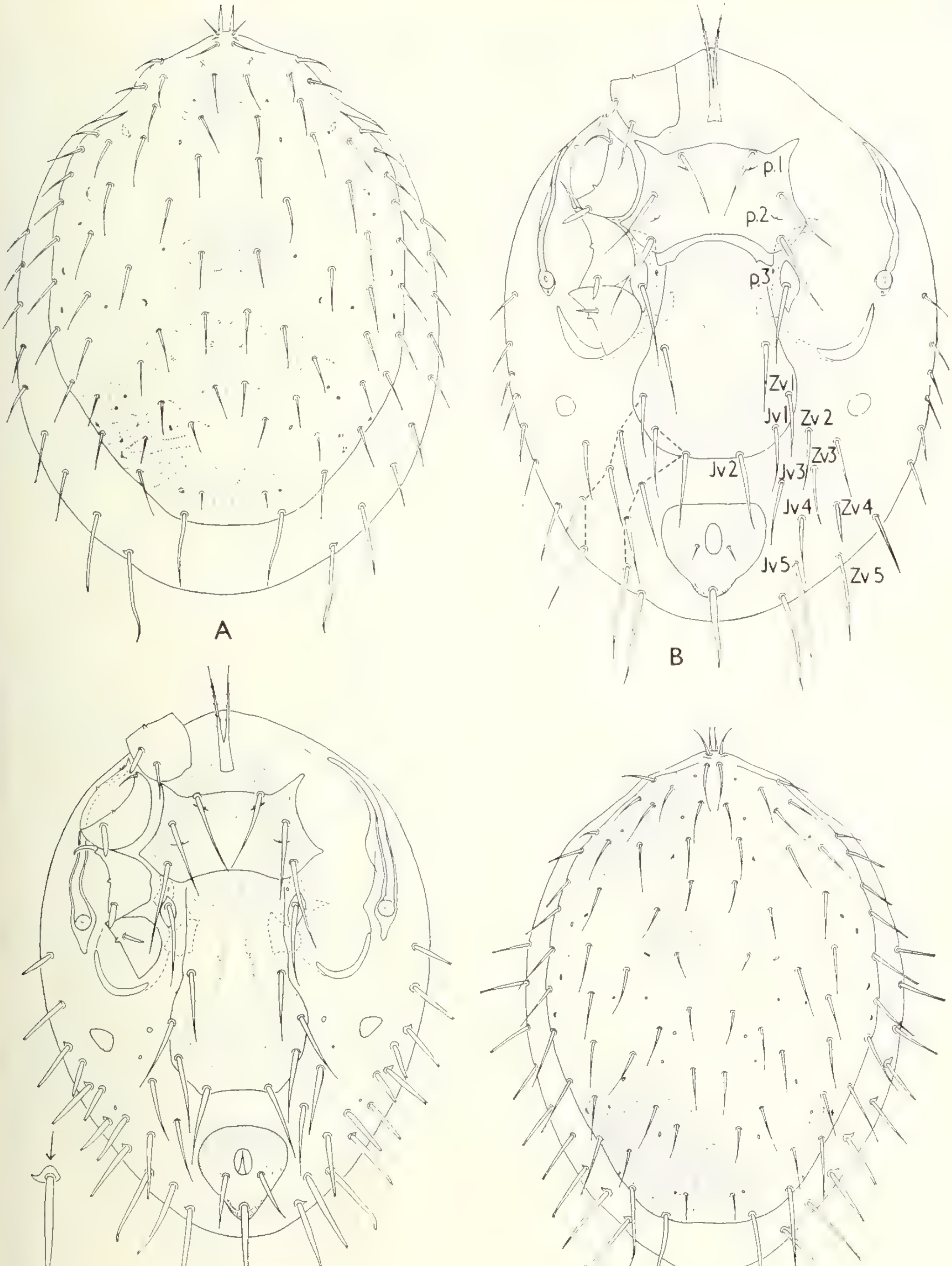
p.1
p.2
p.3
Zv1
Jv1
Zv2
Zv3
Jv2
Jv3
Jv4
Zv4
Jv5
Zv5
A
B
C
D

Fig. 1. A–B. *Laelaps agilis* Koch, female ; dorsum (A) and venter (B) of idiosoma. C–D. *Laelaps hilaris* Koch, female ; venter (C) and dorsum (D) of idiosoma.

malae with inner processes fringed, outer smooth (Text-fig. 2F). Tectum capituli with smooth anterior margin. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (636 μ × 456 μ) with 39 pairs of setae arranged as in Text-fig. 1D; marginal setae longer than the others, especially in the opisthonotal region, and most of them are barbed. Surface of shield reticulated; no hypertrichy; two pairs of *r* and seven pairs of *R* setae on the cuticle, all with bifurcate tips or small barbs.

Tritosternum with base 45 μ, laciniae 102 μ. Sternal shield (102 μ × 186 μ) with three pairs of setae and two pairs of pores; metasternal setae on small platelets, their associated pores on the cuticle. Between *st1*, 80 μ; between *st1* and *st3*, 100 μ. Genital shield (144 μ × 135 μ) flask-shaped, with four pairs of setae. Between *gen.*, 114 μ; between *Jv2*, 80 μ. Anal shield (105 μ × 114 μ), paranal setae 66 μ, postanal seta 96 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 1C. Peritreme extends to posterior margin of coxa I; peritrematal shield free.

Chaetotaxy of legs differs from normal pattern in having two postero-lateral setae on genu IV. On tarsi II and III, setae al_1, pl_1 and av_1 are relatively stout, seta pv_1 is slender. Coxal setae as in Text-fig. 1C. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	66/57	72/60	50/45	80/48
tibia	70/40	57/57	48/45	78/48
tarsus	100/36	90/38	105/36	150/40

Male: Chelicera with segment I, 48 μ; II, 105 μ; movable digit 50 μ (70 μ with spermadactyl); both digits edentate; pilus dentilis as in female, Four pairs of gnathosomal setae with *c.s.* about 48 μ apart; *hyp.2* about 40 μ part. Deutosternum with six transverse rows of denticles (1–3 per row); corniculi 33 μ long. Internal malae, tectum and pedipalps as in female.

Dorsal shield (648 μ × 456 μ) with 39 pairs of setae distributed as in Text-fig. 2G. Surface of shield reticulated; no hypertrichy; two pairs of *r* and five pairs of *R* setae on the cuticle.

Tritosternum with base 45 μ, laciniae 108 μ. Holoventral shield (516 μ × 144 μ) with four pairs of setae and three pairs of pores in the sternal region; six pairs of setae in the genito-ventral region. Between *st1*, 30 μ; between *st1* and *st3*, 102 μ. Paranal setae 45 μ, postanal seta 84 μ. Peritreme extends to posterior margin of coxa I; peritrematal shield fused anteriorly with dorsal shield; posterior part free.

Chaetotaxy of legs as in female. Tarsi II and III with setae al_1, pl_1, av_1, and also av_2, relatively shorter and stouter than the corresponding setae in the female. Tarsus IV has two short, stout, blunt setae, al_1 and pv_1. Coxal setae as in Text-fig. 2H. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	78/66	84/72	63/57	102/66
tibia	75/48	66/64	60/50	96/63
tarsus	102/36	90/40	102/36	147/42

HABITAT : Found mainly on species of the genus *Microtus* in Britain, Europe and the U.S.S.R. Also recorded from a weasel in Germany.

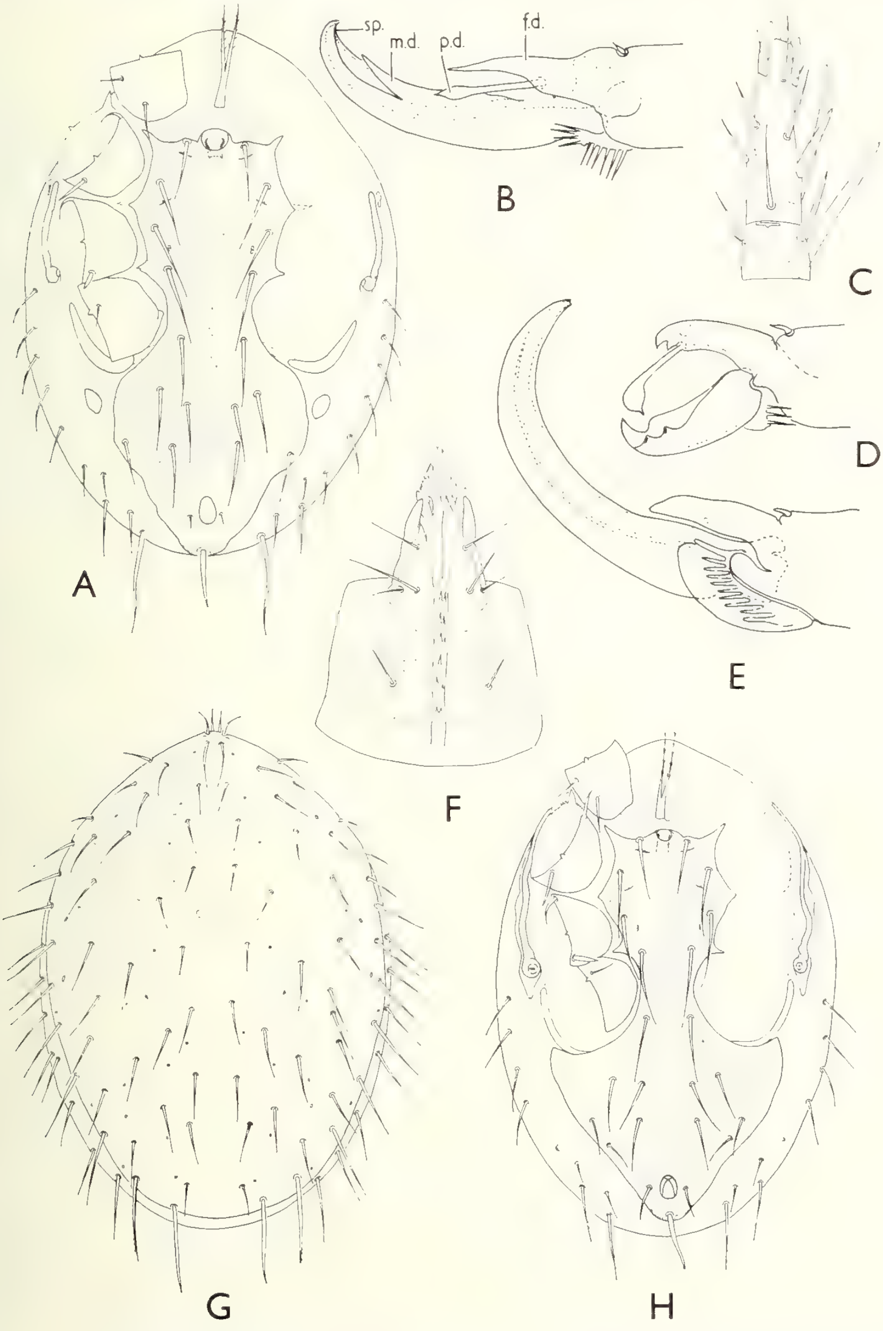

FIG. 2. A. *Laelaps agilis* Koch, venter of male ; B. *Laelaps hilaris* Koch, chelicera of male ; C. *L. agilis*, tarsus IV of male ; D. *L. hilaris*, chelicera of female ; E. *L. agilis*, chelicera of male ; F. *L. hilaris* female, venter of gnathosoma ; G. *L. hilaris* male, dorsum of idiosoma ; H. *L. hilaris* male, venter of idiosoma.

Laelaps agilis Koch

Laelaps agilis Koch, 1836, *Deutschl. C.M.A.* **4** : 19.
Tipton, 1960, *Univ. Calif. Publ. Entomology* **16** : 265, figs.
Laelaps festinus Koch, 1838, *Deutschl. C.M.A.* **24** : 7.
Laelaps hilaroides Oudemans, 1928, *Ent. Ber. Amst.* **7** : 375.
Strandtmann, 1963, *J. Kansas ent. Soc.* **36** : 5, figs. 17–18.

Female : Chelicera with segment I, 66 μ ; II, 123 μ ; movable digit 33 μ, bidentate ; fixed digit unidentate ; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart ; *hyp.* 2 about 45 μ apart. Deutosternum with seven transverse rows of denticles (1–2 per row) ; corniculi 27 μ long ; internal malae with smooth margins. Tectum capituli with free margin rounded, smooth ; salivary styli conspicuous, extending a little beyond tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (636 μ × 456 μ) with 39 pairs of setae distributed as in Text-fig. 1A. Setae $Z5$ considerably longer and stouter than $J5$ or $S5$. Surface of shield reticulate ; no hypertrichy. Cuticle with two pairs of r and seven pairs of R setae.

Tritosternum with base 57 μ, laciniae 100 μ. Sternal shield (123 μ × 192 μ) with three pairs of setae and two pairs of pores ; metasternal setae situated on small shields, their associated pores on the cuticle. Between *st*1, 90 μ ; between *st*1 and *st*3, 114 μ. Genital shield (147 μ × 168 μ) flask-shaped, with four pairs of setae. Between *gen.*, 126 μ ; between *Jv*2, 72 μ. Anal shield (110 μ × 144 μ) with paranal setae 27 μ, postanal seta 105 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 1B. Peritreme extends to anterior third of coxa II ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs differs from normal pattern in that genu IV bears a postero-ventral seta and two postero-lateral setae (2—$\frac{2}{1}$, $\frac{3}{1}$—2). Femur I bears extremely long dorsal setae (ad_1 and pd_1) ; on tarsus II, setae al_1 and pl_1, and on tarsus III, setae al_{1-3} are stout ; on tarsus IV setae al_1 and pv_1 are stouter than setae pl_1 and av_1. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	87/63	78/68	50/50	75/48
tibia	72/54	60/60	45/48	72/42
tarsus	90/40	84/42	114/42	153/36

Male : Chelicera with segment I, 50 μ ; II, 120 μ ; spermadactyl about 84 μ long, separate movable digit not present (Text-fig. 2E). Four pairs of gnathosomal setae with *c.s.* about 48 μ apart ; *hyp.*2 about 36 μ apart. Deutosternum with six rows of denticles (1–2 per row) ; corniculi 33 μ long, weakly sclerotized. Internal malae, salivary styli, tectum and pedipalps as in female.

Dorsal shield (612 μ × 432 μ) with 39 pairs of setae as in female. Tritosternum with base 42 μ, laciniae 90 μ. Holoventral shield (516 μ × 162 μ) with four pairs of setae and three pairs of pores in the sternal region ; five pairs of setae in the genitoventral region. Between *st*1, 72 μ ; between *st*1 and *st*3, 114 μ. Paranal setae 18 μ.

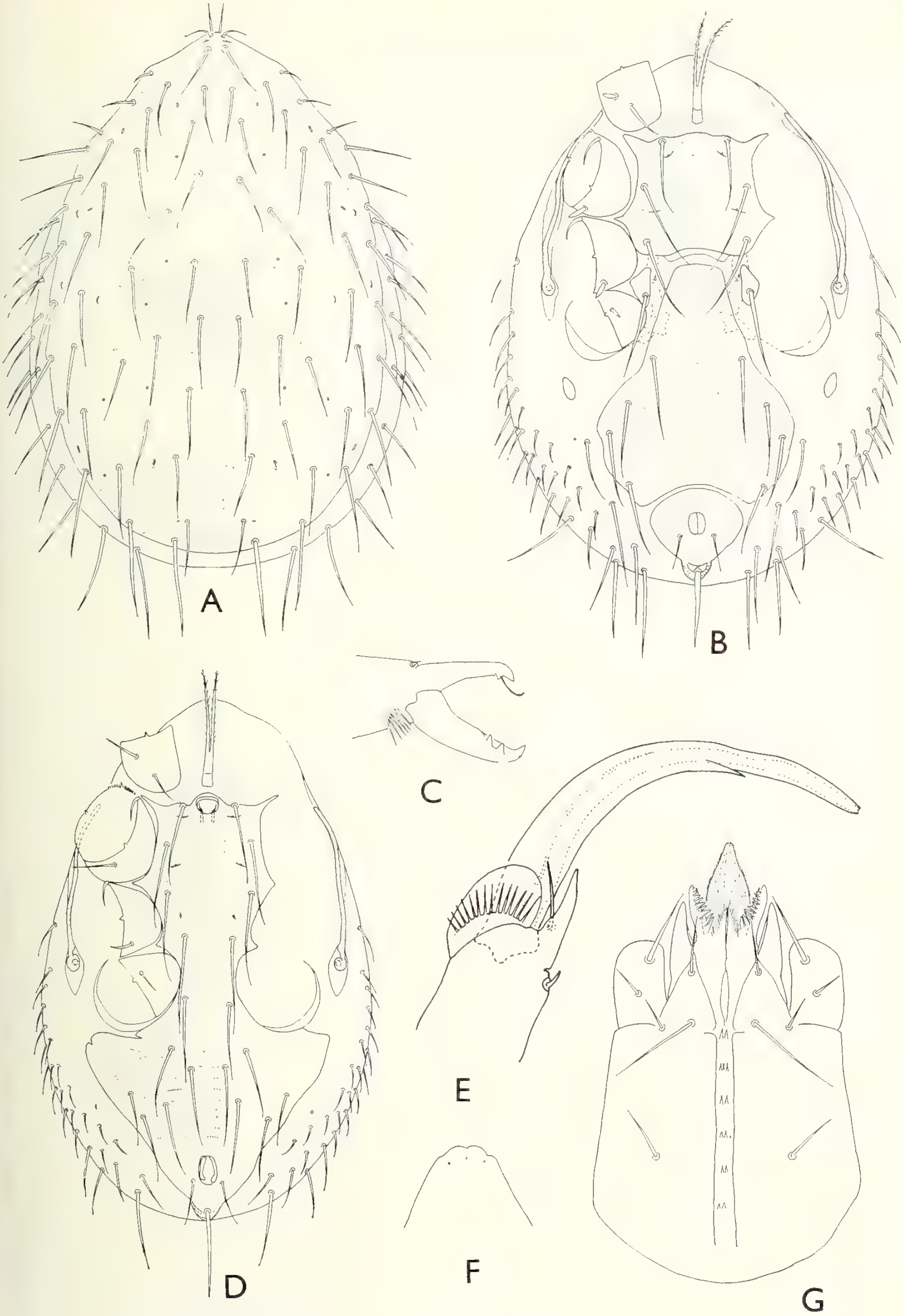

Fig. 3. *Laelaps echidnina* Berlese. A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. chelicera of female; D. venter of idiosoma of male; E. chelicera of male; F. tectum capituli of female; G. venter of gnathosoma of female.

postanal seta 70 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 2A. Peritreme extends to posterior margin of coxa II ; anterior part of peritrematal shield not developed ; posterior part very short, free.

Chaetotaxy of legs as in female. Setae al_1, pl_1 and av_2 on tarsus II, setae al_1 and av_2 on tarsus III, short, stout and blunt. Tarsus IV has setae al_1 and pv_1 stout and blunt ; al_2 and al_3 stout and spine-like ; ad_2 and ad_3 very long, thick and sword-like (Text-fig. 2C). Femur I with setae ad_1 and pd_1 very long and thick. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	80/70	80/66	63/57	87/60
tibia	66/56	60/63	50/54	80/54
tarsus	75/40	80/45	96/42	147/42

HABITAT : Found on *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linn.) in Britain, Europe, Iceland and the U.S.S.R. *L. hilaroides* was recorded from a bat, *Eptesicus serotinus* (Schreber) in Germany.

Laelaps echidnina Berlese

Laelaps (Iphis) echidninus Berlese, 1887, *Acari, Myr. Scorp. Ital.* fasc. 39, no. 1.
Echinolaelaps echidninus : Strandtmann & Mitchell, 1963, *Pacific Insects* **5** : 547, fig. 1.
Laelaps pallidus Trägårdh, 1931, *Nat. Hist. Juan Fernandez* **3** : 616, figs. 145–147.
Laelaps berlesei Fonseca, 1939, *Mem. Inst. Butantan* **12** : 104.
Echinolaelaps echidninus vitzthumi Turk, 1950, *Parasitology* **40** : 71, fig. 7.
Echinolaelaps hirsti Turk, 1950 (nom. nov. pro *L. echidninus* Hirst, 1913, non Berlese, 1887), *Parasitology* **40** : 72, fig. 6.
Echinolaelaps hirsti ceylonicus Turk, 1950, *Parasitology* **40** : 72, figs. 9–10.
Echinolaelaps flavioi Tipton 1960, *Univ. Calif. Publ. Ent.* **16** : 288.

Female : Chelicera with segment I, 120 μ ; II, 228 μ ; movable digit 72 μ, bidentate ; fixed digit unidentate (Text-fig. 3C) ; pilus dentilis long and slender. Four pairs of gnathosomal setae with *c.s.* about 96 μ apart ; *hyp.2* about 84 μ apart. Deutosternum with six transverse rows of denticles (2–3 per row) ; corniculi 54 μ long ; internal malae fringed (Text-fig. 3G). Tectum capituli with smooth anterior margin (Text-fig. 3F). Salivary styli conspicuous, reaching tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (1008 μ × 648 μ) with the normal 39 pairs of setae distributed as in Text-fig. 3A ; no hypertrichy. Surface of shield reticulate ; with eleven pairs of *R* setae on the cuticle. Marginal setae on scutum and cuticle barbed.

Tritosternum with base 84 μ, laciniae 192 μ. Sternal shield (234 μ × 240 μ) extends to middle of coxa III, with three pairs of setae and two pairs of pores. Metasternal setae situated on small shields, associated pores on cuticle. Between *st*1, 132 μ ; between *st*1 and *st*3, 204 μ. Genital shield (258 μ × 216 μ) greatly expanded behind coxae IV (maximum width 396 μ), bearing four pairs of setae.

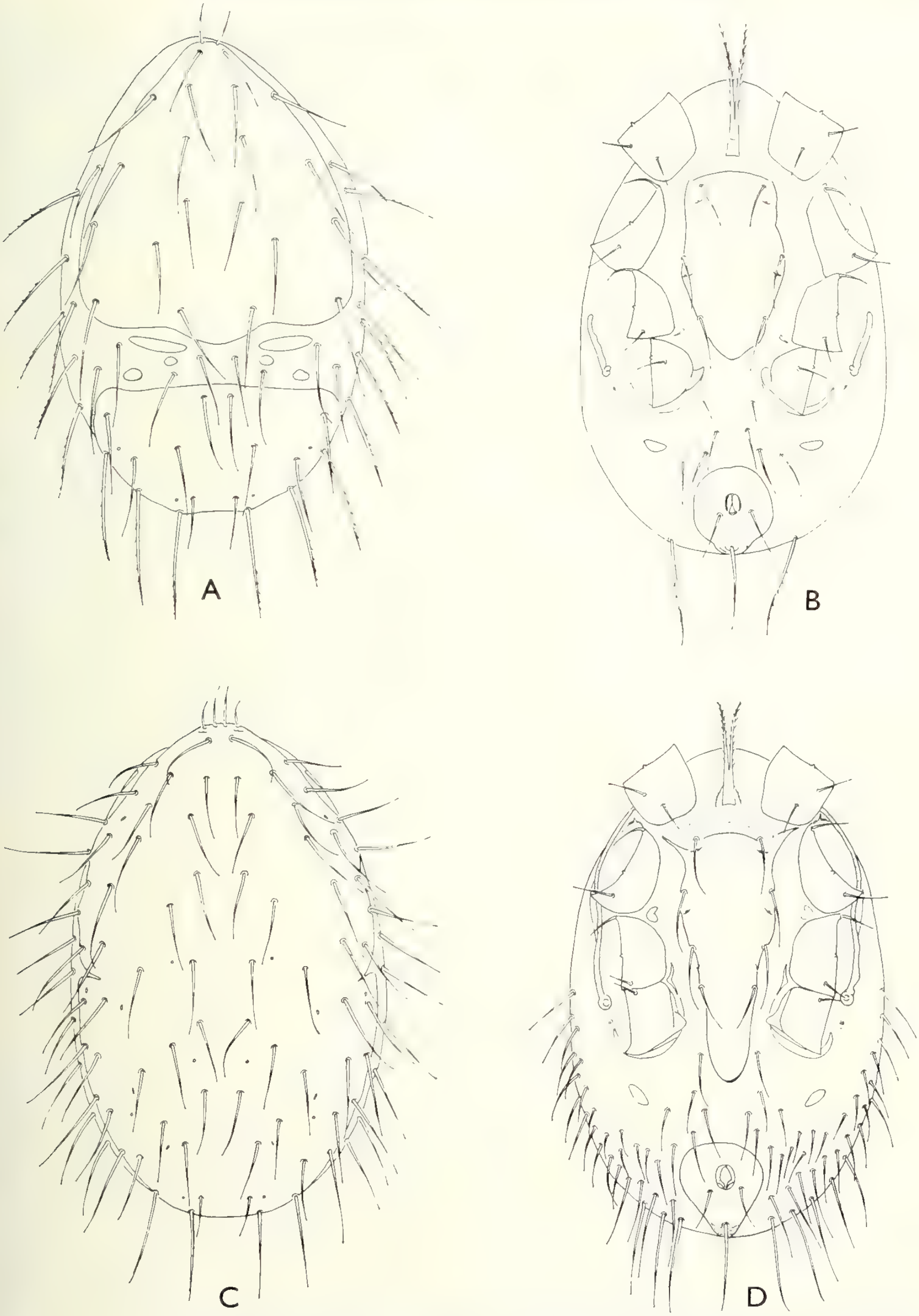

FIG. 4. *Laelaps echidnina* Berlese. A. Dorsum of idiosoma of protonymph ; B. venter of idiosoma of protonymph ; C. dorsum of idiosoma of deutonymph ; D. venter of idiosoma of deutonymph.

Between *gen*, 180 μ; between *Jv2*, 276 μ. Anal shield (168 μ × 190 μ), paranal setae 72 μ, postanal seta 162 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 3B. Peritreme extends to posterior margin of coxa I; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs differs from normal pattern only in having two postero-lateral setae on genu IV. Setae on tarsi II–IV thick and spine-like; the following setae are stout and blunt: al_1 and pl_1 on tarsus II, al_{1-2} on tarsus III, al_1 on tarsus IV. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	120/75	120/90	99/72	117/66
tibia	120/57	108/78	102/66	129/63
tarsus	165/48	150/54	192/50	270/50

Male: Chelicera with segment I, 75 μ; II, 126 μ; both digits edentate, movable digit 102 μ; spermadactyl as in Text-fig. 3E. Four pairs of gnathosomal setae with *c.s.* about 66 μ apart; *hyp.2* about 72 μ apart. Deutosternum, tectum and pedipalps as in female; corniculi longer and more attenuate.

Dorsal shield (840 μ × 492 μ) with the normal 39 pairs of setae; no hypertrichy. Surface of shield reticulated; marginal setae on shield and cuticle barbed.

Tritosternum with base 60 μ, laciniae 150 μ. Holoventral shield (684 μ × 174 μ) greatly expanded behind coxae IV, with four pairs of setae and three pairs of pores in the sternal region, six pairs of setae in the genito-ventral region (Text-fig. 3D). Between *st1*, 84 μ; between *st1* and *st3*, 150 μ. Paranal setae 72 μ; postanal seta 140 μ. Peritreme extends to anterior margin of coxa II; anterior part of peritrematal shield fused with dorsal shield from a point a little posterior to the tip of the peritreme; posterior part free.

Chaetotaxy of legs as in female, but stout setae on tarsi II–IV are all pointed. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	120/72	120/84	102/66	114/66
tibia	120/60	108/72	102/60	126/60
tarsus	174/54	144/50	180/48	246/48

Protonymph: Chelicera with segment I, 75 μ; II, 135 μ; movable digit 45 μ, bidentate; fixed digit unidentate. Four pairs of gnathosomal setae with *c.s.* about 66 μ part, *hyp.2* about 70 μ apart. Corniculi 45 μ long; deutosternum with six transverse rows of denticles (1–3 per row); internal malae and tectum as in female. Pedipalp (1–4–5–12) with two-tined apotele.

Podonotal shield (444 μ × 372 μ) with eleven pairs of setae; pygidial shield (192 μ × 350 μ) with eight pairs of setae, the marginal ones being barbed. Chaetotaxy and sclerotization of mesonotal region as in Text-fig. 4A.

Tritosternum with base 60 μ, laciniae 135 μ. Sternal shield (255 μ × 162 μ) with three pairs of setae and two pairs of pores ; between *st*1, 96 μ ; between *st*1 and *st*3, 102 μ. Anal shield (130 μ × 123 μ) with paranal setae 78 μ, postanal seta 144 μ long. Peritreme extends at least to middle of coxa III (Text-fig. 4B).

Chaetotaxy of legs normal ; many of the setae stout and spine-like ; particularly long setae on femora I and II (distal dorsals) and on dorsal surface of genu, tibia and tarsus IV. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	96/78	96/84	78/66	84/60
tibia	100/57	84/72	72/60	84/54
tarsus	168/42	150/48	162/48	207/45

Deutonymph : Chelicera with segment I, 90 μ ; II, 168 μ ; chelae as in female, movable digit 54 μ. Four pairs of gnathosomal setae with *c.s.* about 78 μ apart ; *hyp*.2 about 78 μ apart. Corniculi, deutosternum, internal malae and tectum as in protonymph. Pedipalps as in female.

Dorsal shield (876 μ × 504 μ) with the normal 39 pairs of setae ; six pairs of *R* setae on the cuticle. Marginal setae on shield and cuticle barbed (Text-fig. 4C).

Tritosternum with base 90 μ, laciniae 150 μ. Sternal shield (432 μ × 168 μ) with four pairs of setae and three pairs of pores. Between *st*1, 114 μ ; between *st*1 and *st*3, 192 μ. Anal shield (150 μ × 156 μ) with paranal setae 75 μ, postanal seta 168 μ. Peritreme extends to posterior third of coxa I (Text-fig. 4D).

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	108/70	105/78	87/66	100/60
tibia	114/60	90/72	90/63	108/54
tarsus	174/48	138/54	186/50	228/50

HABITAT : Cosmopolitan, chiefly on rodents of the genus *Rattus*. Also recorded from the genera *Mus* and *Bandicota* and from the tree-shrew, *Tupaia glis* (Diard).

Laelaps muris (Ljungh)

Acarus muris Ljungh, 1799, *Nova Act. Reg. Soc. Sci. Uppsala* **6** : 10.
Laelaps muris : Tipton, 1960, *Univ. Calif. Publ. Ent.* **16** : 277, figs.
Laelaps arvicola George, 1889, *Science Gossip* **25** : 6, figs. 1–2.
Laelaps crassipes Schrank, Oudemans, 1897, *Tijdschr. Ent.* **39** : 135.
Laelaps microti Oudemans, 1916, *Ent. Ber. Amst.* **4** : 309.
Laelaps agilis (Koch) Hirst, 1916, *J. Zool. Res.* **1** : 67.

Female : Chelicera with segment I, 70 μ ; II, 110 μ ; movable digit 32 μ, bidentate ; fixed digit unidentate, pilus dentilis inflated, elongate, tapering abruptly at the tip (Text-fig. 5E). Four pairs of gnathosomal setae with *c.s.* about 78 μ apart, *hyp*.2 about 54 μ apart. Deutosternum with six rows of deutosternal denticles (1–2

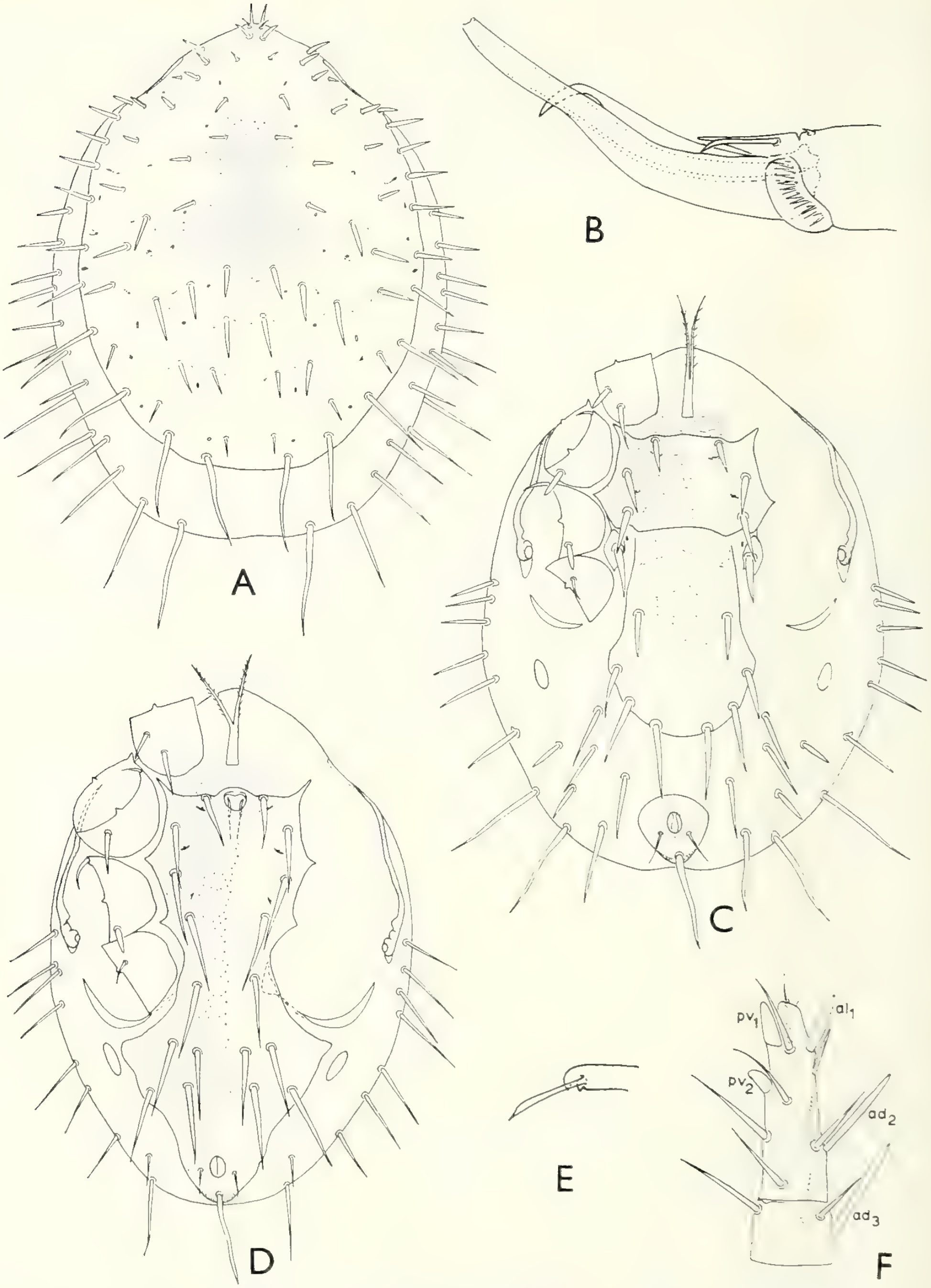
A
B
C
D
E
F
pv_1
al_1
pv_2
ad_2
ad_3

FIG. 5. *Laelaps muris* (Ljungh). A. Dorsum of idiosoma of female; B. chelicera of male; C. venter of idiosoma of female; D. venter of idiosoma of male; E. pilus dentilis of female; F. tarsus IV of male, ventral view.

per row); corniculi 30 μ long; internal malae with inner processes fringed, outer smooth. Tectum capituli with free margin rounded, smooth. Salivary styli extend slightly beyond tips of corniculi. Pedipalp (2–5–6–14) with two tined apotele.

Dorsal shield (660 μ × 492 μ) with 39 pairs of setae distributed as in Text-fig. 5A. Most setae short and spine-like, setae *Z*5 and *S*3–5 at least twice as long as seta *J*1. Surface of shield granular, weakly reticulate laterally; no hypertrichy; two pairs of *r* and ten pairs of *R* setae on the cuticle.

Tritosternum with base 60 μ, laciniae 126 μ. Sternal shield (144 μ × 222 μ) with three pairs of short, spine-like setae and two pairs of pores; metasternal setae on small shields, associated pores on cuticle. Between *st*1, 93 μ; between *st*1 and *st*3, 120 μ. Genital shield (180 μ × 174 μ) flask-shaped with four pairs of setae; between *gen.*, 140 μ; between *Jv*2, 84 μ. Anal shield (96 μ × 110 μ) with paranal setae 63 μ, postanal seta 168 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 5C. Peritreme extends beyond posterior margin of coxa I; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs differs from normal pattern in that genu IV has two posterolateral setae, seta pl_2 being considerably shorter than pl_1; tarsi II–IV with setae ad_1 and pd_1. Femur I with setae ad_1 and pd_1 stout and sinuous, the latter very long. Setae av_1, al_1 and pl_1 on tarsi II and III stout and blunt. Setae al_2 and al_3 on tarsus III and the ventral and lateral setae on tarsus IV stout and spine-like. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	90/70	90/70	60/54	102/54
tibia	75/58	66/63	50/50	90/50
tarsus	96/45	90/48	114/42	153/42

Male: Chelicera with segment I, 48 μ; II, 87 μ; both digits edentate; movable digit about 70 μ long, 84 μ with spermadactyl (Text-fig. 5B). Four pairs of gnathosomal setae with *c.s.* about 63 μ apart; *hyp.*2 about 48 μ apart. Corniculi 33 μ long; salivary styli extend approximately to tips of corniculi. Deutosternum, internal malae, tectum and pedipalps as in female.

Dorsal shield (636 μ × 462 μ) with 39 pairs of setae; one pair of *r* and six pairs of *R* setae on the cuticle. Tritosternum with base 45 μ, laciniae 114 μ. Holoventral shield (546 μ × 180 μ) with four pairs of setae and three pairs of pores in the sternal region; five pairs of setae in the genito-ventral region. Between *st*1, 78 μ; between *st*1 and *st*3, 108 μ. Paranal setae 36 μ, postanal seta 130 μ. Surface of shield reticulate and granular. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 5D. Peritreme extends to posterior margin of coxa I; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs and form of setae as in female. In addition, seta av_2 on tarsus II is stout and blunt. Tarsus IV with setae pv_1 and pv_2 stout and blunt; setae al_1, ad_2 and ad_3 stout and blade-like (Text-fig. 5F), genu and tibia IV each with a stout blade-like seta al_2. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	90/63	90/78	66/60	114/66
tibia	75/54	66/66	57/57	99/63
tarsus	93/44	84/45	105/45	140/45

HABITAT: Found in Britain, Europe and the U.S.S.R., mainly on *Arvicola terrestris* (Linn.). Also recorded from *Microtus arvalis* (Pallas) and *Talpa europaea* Linn.

Genus ***HYPERLAELAPS*** Zachvatkin

Hyperlaelaps Zachvatkin, 1948, *Parazit. Sb.* **10** : 61.

Type: *Tetragonyssus microti* Ewing, 1933.

Small, medium sclerotized mites ranging from 500 to 600 μ in length. Chelicerae chelate-dentate in the female with the movable digit bidentate. Fixed digit in the male markedly reduced, edentate; movable digit entirely fused with the extremely elongated spermadactyl. Pilus dentilis long, not inflated distally. Dorsal seta and fissures normal. Arthrodial processes at base of movable digit in female few in number and long. Chaetotaxy of venter of gnathosoma normal; chaetotaxy of pedipalp deficient (2–4/5–6–13/14); apotele two-tined. Deutosternum with six or seven rows of denticles, one or two denticles per row. Corniculi horn-like. Tectum membranous, with rounded or lobate anterior margin, never denticulate.

Dorsal shield entire and with 37 (*px2* and *px3* lacking) or 38 (*px3* lacking) pairs of setae. Majority of dorsal setae short and subspinose.

Tritosternum normal, bipartite. No definite pre-endopodal shields. Sternal shield in female with three pairs of setae and two pairs of pores; metasternal setae on distinct shields. Genito-ventral shield inflated posterior to coxae IV and bearing four pairs of setae. Anal shield truncate anteriorly with normal setation. Opisthogastric cuticle with a maximum of twelve pairs of setae; male with fewer setae than the female. Peritrematal shield poorly developed, free posteriorly. Metapodal shields present. Male with sternito-genito-ventral shield bearing ten pairs of setae, anal shield free. Podal shields weakly developed posterior to coxae IV.

Chaetotaxy of legs normal except genu III ($2—\frac{2}{1}, \frac{2}{0}—1$), tibia III in *H. amphibia* ($1—\frac{1}{1}, \frac{2}{1}—1$) and genu IV ($2—\frac{2}{1}, \frac{3}{0}—2$). Femora I and II in both sexes with ad_1 at least three times the length of pd_1. Coxa II with anterior spine.

Zachvatkin (1948) proposed *Hyperlaelaps* as a subgenus of *Laelaps* with *Laelaps* (*Hyperlaelaps*) *arvalis* Zachvatkin as the type. In recent revisionary works on this group (Strandtmann & Wharton, 1958 and Tipton, 1960) this subgenus has been synonymized with *Laelaps*. Detailed studies of the chaetotaxy of the species included in *Hyperlaelaps* have shown that they are not congeneric with the species of *Laelaps*.

There is some confusion, at present, concerning the name of the type species. Koch (1839) described *Laelaps pachypus* from the field mouse (" *Lemnus arvalis* "), believing it to be conspecific with *Acarus pachypus* Hermann, 1804. The first accurate description and figure of *Laelaps pachypus* sensu Koch may be attributed to Hirst (1916). Later Oudemans (1927), without reference to Hirst, re-described both sexes of what he considered to be *Laelaps pachypus* sensu Koch. Unfortunately two related species are confused in his description, the male (from *Microtus arvalis*) being referable to *Laelaps pachypus* sensu Hirst, and the female (from *Arvicola amphibius*) to a species which has subsequently been described as *Laelaps* (*Hyperlaelaps*) *amphibius* by Zachvatkin (1948). We have examined Oudemans' material of *L. pachypus* and can confirm that these two species were represented in the material he had before him in 1927. In 1936 Oudemans correctly pointed out that Koch (1839) has misidentified *Acarus pachypus* Hermann and proposed a new name, *Laelaps kochi*, for *Laelaps pachypus* sensu Koch. On the basis of the type host and of the figures of *pachypus* by Hirst (1916) we consider *L.* (*H.*) *arvalis* Zachvatkin to be a synonym of *Laelaps kochi* Oudemans.

Recently we have had the opportunity, through Dr. Crabill, Smithsonian Institution, of examining the " cotype " material of *Tetragonyssus microti* Ewing from *Microtus californicus*, Los Angeles, California, and from *Microtus* sp., Alaska. We are unable to separate morphologically Ewing's species from *Laelaps kochi* Oudemans taken from *Microtus arvalis* in Britain. We therefore consider *L. kochi* to be synonymous with *T. microti*.

Key to Males and Females

1 Tibia III with chaetotactic formula $(2-\frac{1}{1}, \frac{2}{1}-1)$. Palpfemur with five setae. Dorsal shield with setae *px*2 present or absent. In the female, seta *s*6 short and spinose, seta *S*1 relatively long and slender . **H. microti** (Ewing) (p. 141)
– Tibia III with chaetotactic formula $(1-\frac{1}{1}, \frac{2}{1}-1)$. Palpfemur with four setae. Dorsal shield usually with setae *px*2 present. In the female, seta *s*6 and *S*1 both short and spinose . . . . **H. amphibia** Zachvatkin (p. 144)

Hyperlaelaps microti (Ewing)

Laelaps pachypus Koch, 1839, *Deutschl. C.M.A.* **24** : 8 (non *Acarus pachypus* Hermann, 1804).
Hirst, 1916, *J. Zool. Res.* **1** (2) : 68, figs. 5–6.
Oudemans, 1927, *Tijdschr. Ent.* **70** : 179 (in part).
Tetragonyssus microti Ewing, 1933, *Proc. U.S. nat. Mus.* **82** (art. 30) : 9.
Laelaps kochi Oudemans, 1936, *Krit. Hist. Over. Acar.* **3** (A) : 244 (nom. nov. for *L. pachypus* *Koch*). [in part].
Laelaps (*Hyperlaelaps*) *arvalis* Zachvatkin, 1948, *Parazit. Sb.* **10** : 74, figs. 25–26 (**syn. nov.**).

Female : Chelicera with segment I, 54 μ ; II, 140 μ ; movable digit 36 μ, bidentate ; fixed digit unidentate, pilus dentilis elongate, broad, not inflated distally (Text-fig. 7B). Four pairs of gnathosomal setae with *c.s.* about 66 μ apart, *hyp*.2 about 48 μ apart. Deutosternum with seven rows of denticles (1–2 per row) ; corniculi 42 μ long ; internal malae with smooth margins. Tectum capituli with free margin rounded or slightly lobed in appearance. Pedipalp (2–5–5–13) with two-tined apotele.

Dorsal shield (588 μ × 444 μ) with 37 pairs of setae distributed as in Text-fig. 6A, the setae of the *px* series being absent, more rarely *px*2 present paired or unpaired.

Surface of shield granular, reticulate laterally ; no hypertrichy ; six pairs of *R* setae on the cuticle. Most of the setae are short and spine-like ; those of the *S* series and seta *Z*5 are considerably longer. Seta *s*6 short and spine-like.

Tritosternum with base 45 μ, laciniae 110 μ. Sternal shield (70 μ × 192 μ) with posterior margin deeply concave, lateral margins heavily sclerotized ; with three

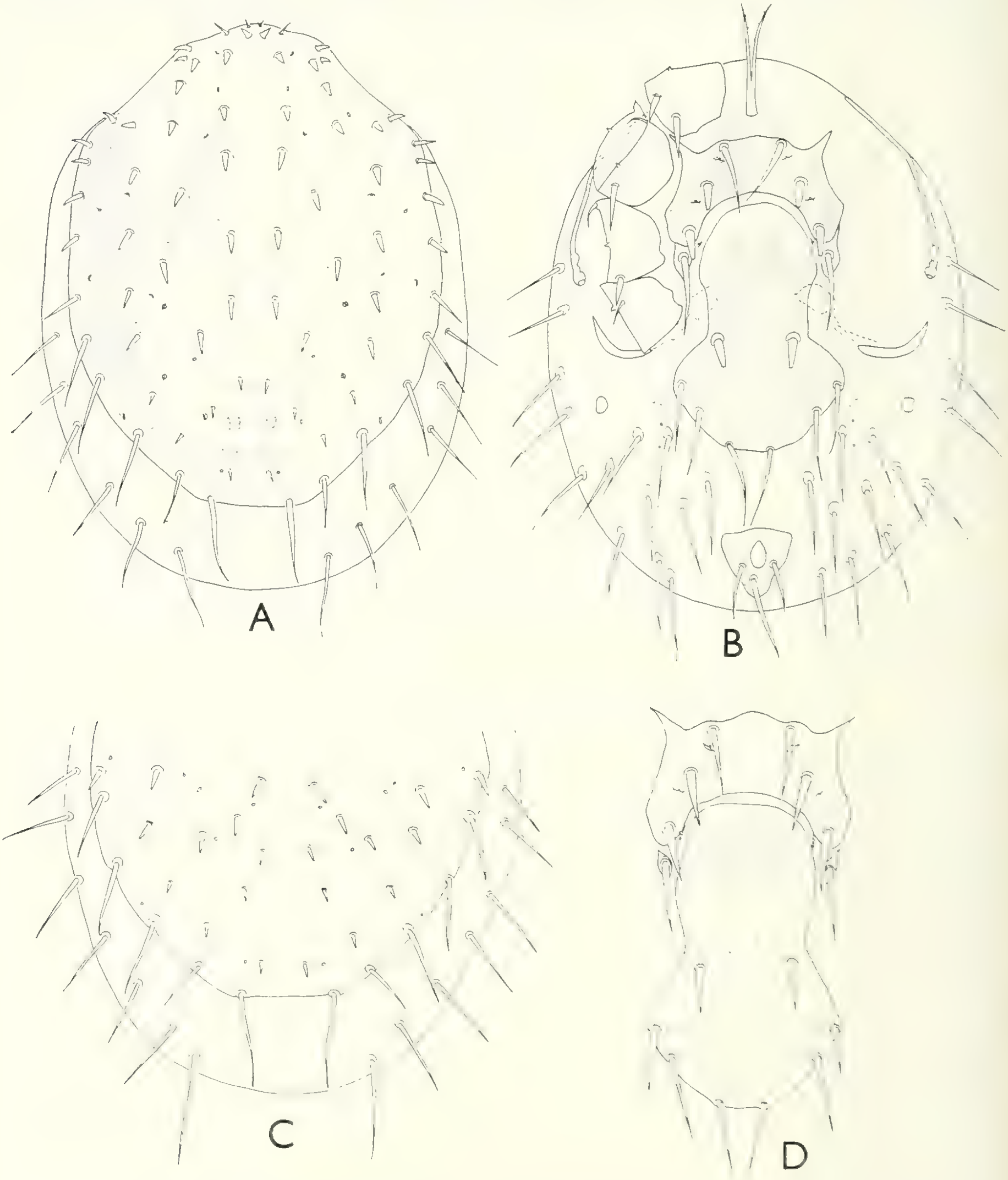

Fig. 6. A–B. *Hyperlaelaps microti* (Ewing), female ; dorsum (A) and venter (B) of idiosoma. C–D. *Hyperlaelaps amphibia* Zachvatkin, female ; opisthonotal region (C) ; sternal and genito-ventral shields (D).

pairs of setae and two pairs of pores. Setae 2 and 3 are short, with unevenly truncate tips which give the appearance of being broken; metasternal setae situated on small shields, associated pores on cuticle. Between *st*1, 70 μ; between *st*1 and *st*3, 117 μ. Genital shield flask-shaped (135 μ × 135 μ), with four pairs of setae, expanded behind the genital setae and reaching its maximum width (216 μ) at level of *Zv*1. Between the short, truncate *gen.*, 96 μ; between *Jv*2, 50 μ. Anal shield (70 μ × 78 μ) with maximum width (87 μ) at anterior margin. Paranal setae 78 μ, postanal seta 108 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 6B, the setae being situated on small projections of the integument. Peritreme extends to posterior margin of coxa I; anterior part of peritrematal shield fused with dorsal shield; posterior part not visible.

The chaetotaxy of the legs differs from the normal pattern in three respects: genu III lacks seta *pv*; genu IV has seta pl_2; tarsi II–IV lack setae ad_1 and pd_1. Femur I with seta ad_1 at least three times as long as pd_1; femur II with seta ad_1 about three times as long as pd_1. Many of the leg setae are reduced to short spines. Trochanter I with pv_2 short and stout; genu I with ad_3 and pd_3 relatively long and thick; trochanters III and IV with *al* and *d* stout; femur IV with ad_1 long and stout; tarsi II–IV with ventral and lateral setae relatively stout, tapering. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	80/84	84/72	54/57	90/57
tibia	69/63	57/69	45/54	80/50
tarsus	78/45	96/45	93/42	144/42

Male: Chelicera with segment I, 42 μ; II, 75 μ; spermadactyl 150 μ; movable digit not visible (Text-fig. 7C). Four pairs of gnathosomal setae with *c.s.* about 57 μ apart; *hyp.*2 about 42 μ apart. Corniculi about 40 μ long, weakly sclerotized, membranous. Internal malae difficult to distinguish. Deutosternum, tectum and pedipalps as in female.

Dorsal shield (504 μ × 360 μ) with 37 pairs of setae as in female; seven pairs of *R* setae on the cuticle.

Tritosternum with base 36 μ; laciniae 90 μ. Sternito-genito-ventral shield (324 μ × 150 μ) with four pairs of setae and three pairs of pores in sternal region, six pairs of setae in genito-ventral region. Between *st*1, 54 μ; between *st*1 and *st*3, 102 μ. Anal shield (60 μ × 70 μ) with maximum width (80 μ) at anterior margin. Paranal setae 48 μ, postanal seta 75 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 7A. Peritreme extends about to anterior margin of coxa II; anterior part of peritrematal shield fused with dorsal shield; posterior part not developed.

Chaetotaxy of the legs as in female. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	78/72	75/63	50/56	80/50
tibia	60/57	54/63	42/48	75/45
tarsus	72/42	80/42	84/40	132/40

HABITAT: Found in Britain on *Microtus arvalis* (Pallas), *M. agrestis* (Linn.) and *M. orcadensis* Millais. Recorded from Europe and the U.S.S.R. from the genus *Microtus*, from *Rattus rattus* (Linn.), *Apodemus sylvaticus* (Linn.) and "*Mustela vulgaris*".

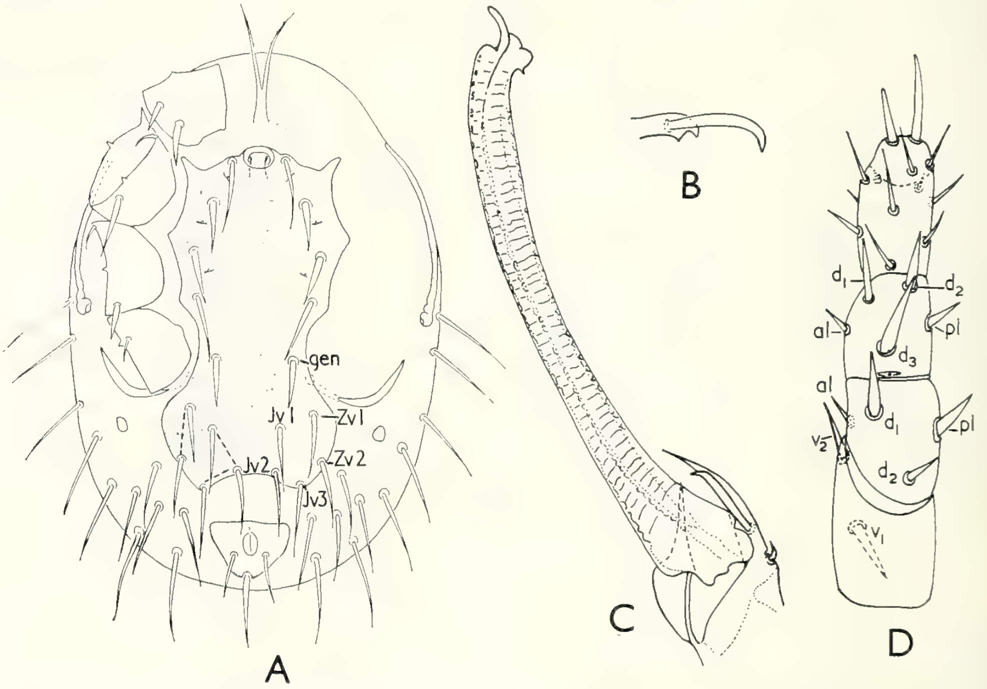

FIG. 7. A–C. *Hyperlaelaps microti* (Ewing); venter of idiosoma of male (A); pilus dentilis of female (B); chelicera of male (C). D. *Hyperlaelaps amphibia* Zachvatkin, female; right pedipalp (trochanter to tibia), dorsal view.

Hyperlaelaps amphibia Zachvatkin

Laelaps (*Hyperlaelaps*) *amphibius* Zachvatkin, 1948, *Parazit. Sb.* **10**: 74, figs. 22–24.
Laelaps pachypus (Koch) Oudemans, 1927, *Tijdschr. Ent.* **70**: 179 (in part).

Female: Chelicera with segment I, 50 μ; II, 153 μ; movable digit 36 μ, bidentate; fixed digit unidentate, pilus dentilis elongate, band-like, with pointed tip. Four pairs of gnathosomal setae with *c.s.* about 66 μ apart, *hyp.*2 about 54 μ apart. Deutosternum with six rows of denticles (1–2 per row); corniculi 30 μ long. Internal malae and tectum capituli as in *H. microti*. Pedipalp (2–4–5–13) with two-tined apotele (Text-fig. 7D).

Dorsal shield (600 μ × 408 μ) with 38 pairs of setae, *px*2 being present (Text-fig. 6C). Setae *s*6 and *S*1 both short and spine-like. Surface of shield granular, reticulate laterally; seven pairs of *R* setae on the cuticle.

Tritosternum with base 42 μ, laciniae 117 μ. Sternal shield (84 μ × 192 μ) with setae 2 and 3 longer and more pointed than in *H. microti* (Text-fig. 6D); between *st*1, 78 μ; between *st*1 and *st*3, 123 μ. Metasternal setae on small platelets, associated pores on cuticle, very close to sternal shield. Genital shield (150 μ × 162 μ) with maximum width (216 μ) at level of *Zv*1; between *gen.*, 102 μ; between *Jv*2, 60 μ. Genital setae (*gen.*) more pointed than in *H. microti* (Text-fig. 6D). Anal shield (60 μ × 78 μ) with maximum width (102 μ) at anterior margin. Paranal setae 60 μ, postanal seta 96 μ long. Peritremes and chaetotaxy and sclerotization of opisthogaster as in *H. microti*.

Chaetotaxy of legs as in *H. microti* except that tibia III bears only one anterolateral seta. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	90/75	90/84	54/63	90/54
tibia	66/60	60/72	40/54	84/45
tarsus	72/45	93/48	87/45	150/42

Male: Chelicera with segment I, 42 μ; II, 120 μ; spermadactyl 168 μ, movable digit not visible. Four pairs of gnathosomal setae with *c.s.* about 63 μ apart; *hyp.*2 about 48 μ apart Corniculi about 54 μ long, weakly sclerotized. Internal malae difficult to distinguish. Deutosternum, tectum capituli and pedipalps as in female.

Dorsal shield (552 μ × 396 μ) with 38 pairs of setae as in female. Tritosternum with base 33 μ, laciniae 90 μ. Sternito-genito-ventral shield (372 μ × 168 μ) as in *H. microti*. Between *st*1, 63 μ; between *st*1 and *st*3, 102 μ. Anal shield (63 μ × 75 μ) with maximum width (90 μ) at anterior margin. Paranal setae 45 μ, postanal seta 90 μ long. Chaetotaxy and sclerotization of opisthogaster as in *H. microti*. Peritreme extends to middle of coxa II.

Chaetotaxy of legs and form of setae as in female. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	78/72	84/70	60/63	80/48
tibia	66/63	54/66	45/54	80/42
tarsus	72/48	84/45	90/45	135/38

HABITAT: Recorded from Britain, Europe and the U.S.S.R. on *Arvicola terrestris* (Linn.)

Genus ***ONDATRALAELAPS*** Evans & Till

Ondatralaelaps Evans & Till, 1965, *Bull. Brit. Mus. (nat. Hist.) Zool.* **13**: 269.

Type: *Laelaps multispinosa* Banks, 1909.

Medium sclerotized mites ranging from 650 μ to 750 μ in length and with the general facies of *Laelaps*. Chelicerae chelate-dentate in the female with the broad movable digit bidentate and the shorter fixed digit unidentate. Fixed digit in the male markedly reduced, edentate, movable digit partially fused with elongate grooved

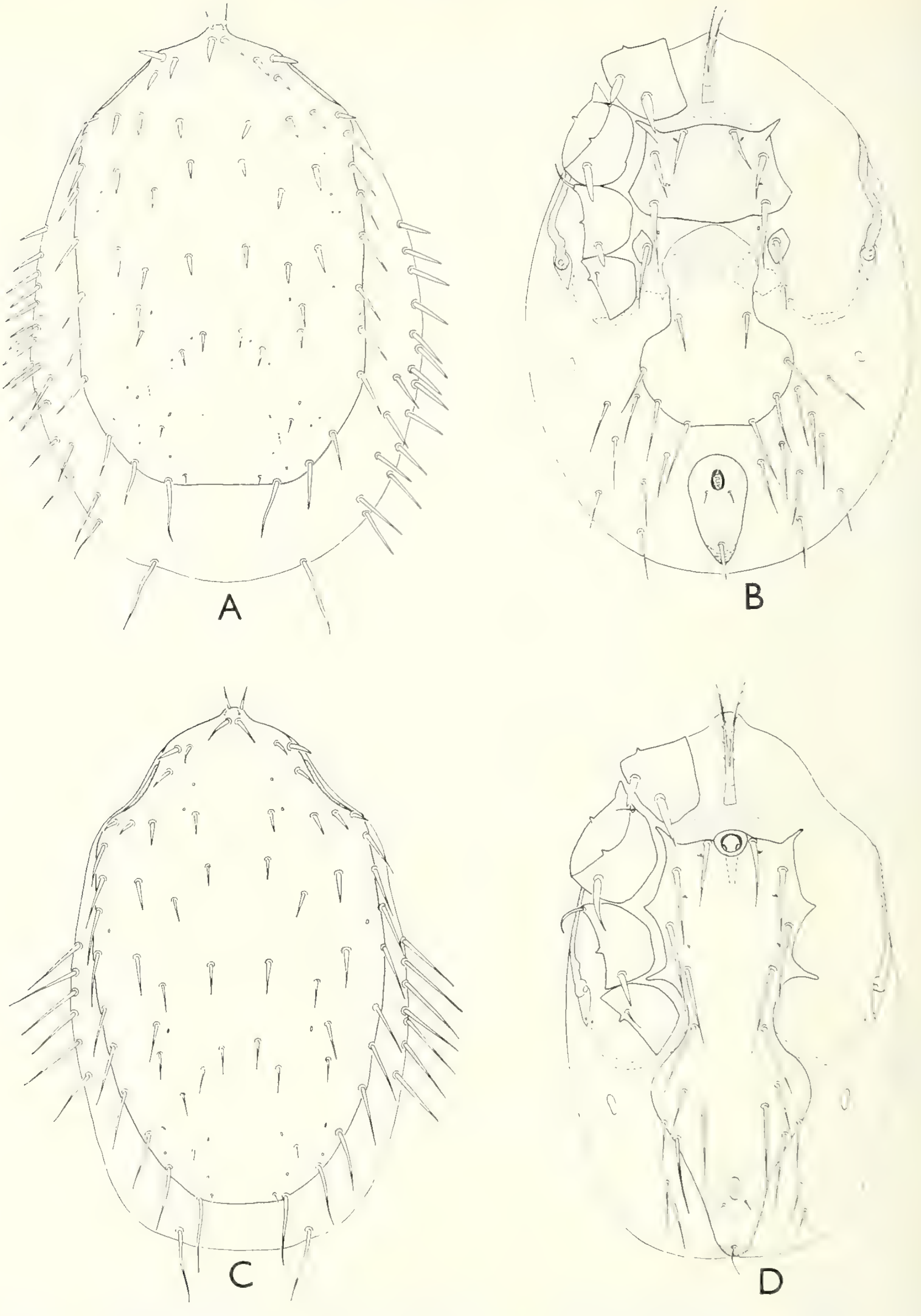

FIG. 8. *Ondatralaelaps multispinosa* (Banks). A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. dorsum of idiosoma of male ; D. venter of idiosoma of male.

spermadactyl. Pilus dentilis long, hooked distally. Dorsal seta and fissures normal. Arthrodial processes at base of movable digit present. Chaetotaxy of the venter of the gnathosoma normal ; chaetotaxy of pedipalp deficient (2–5–5–14) ; apotele two-tined. Deutosternum with six transverse rows of denticles, one to three denticles per row. Corniculi horn-like ; internal malae fimbriated. Tectum capituli tongue-shaped, margin smooth.

Dorsal shield entire with typically 32 pairs of setae, podonotal region with 20 pairs of setae, opisthonotal region with 12 pairs (*j*3, *z*3, *J*3, *J*4, *Z*3, *px*2 and *px*3 lacking in comparison with the typical form in *Laelaps*). Intraspecific variation of the opisthonotal chaetotaxy common. Dorsal setae in the female shorter and stouter than in the male. Sexual dimorphism affecting form and number of marginal setae (r and *R*) in the adult.

Tritosternum normal, bipartite. No definite pre-endopodal shields. Sternal shield in the female with three pairs of setae and two pairs of pores, metasternal setae on discrete platelets. Genito-ventral shield typically *Laelaps* with four pairs of setae. Anal shield elongate-oval in outline, paranal setae situated behind the anus. Opisthogastric cuticle with up to ten setae, variable. Peritrematal shields free posteriorly. Small metapodal shields present. Male with holoventral shield bearing nine pairs of setae excluding anals. Opisthogastric cuticle with about two pairs of setae. Podal shields weakly developed posterior to coxae IV.

Chaetotaxy of legs normal except for genu III (2—$\frac{2}{1}$, $\frac{2}{0}$—1) and genu IV (2—$\frac{2}{1}$, $\frac{3}{0}$—2). Coxa II with well-developed anterior spine. Femur I with ad_1 and pd_1 very stout and long, pd_1 arising from sclerotized protuberance (Text-fig. 9D). Certain setae on other segments tend to be stout. Ambulacra with claws reduced or absent.

Two species are included in this genus, the type species occurring on the Musk Rat, *Ondatra zibethica* (Linn.) in North America and Europe (introduced), and *Ondatralaelaps evansi* (Tipton) *comb. nov.* from the Southern Musk Rat, *Neofiber alleni* True in Florida, U.S.A.

Ondatralaelaps multispinosa (Banks)

Laelaps multispinosus Banks, 1909, *Proc. ent. Soc. Wash.* **11** : 136 ; Bregetova, 1956, *Opred. Faune SSSR.* **61** : 105.
Liponyssus spiniger Ewing & Stover, 1915, *Ent. News* **26** (3) : 109.
Tetragonyssus spiniger: Ewing, 1922, *Proc. U.S. nat. Mus.* **62** (art. 13) : 10.
Laelaps parvanalis Willmann, 1952, *Z. Parasitenk.* **15** (5) : 398.

Female : Chelicera with segment I, 57 μ ; II, 117 μ ; movable digit 36 μ, bidentate ; fixed digit reduced in size, with a terminal hook, pilus dentilis extremely elongate (Text-fig. 9E). Four pairs of gnathosomal setae with *c.s.* about 66 μ apart, *hyp*.2 about 60 μ apart. Deutosternum with six transverse rows of denticles (one to three denticles per row) ; corniculi horn-like, 30 μ long ; internal malae fimbriate (Text-fig. 9F). Tectum capituli tongue-shaped with anterior margin rounded, smooth. Pedipalp (2–5–5–14) with two-tined apotele.

Dorsal shield (696 $\mu \times$ 432 μ) with 32 pairs of setae distributed as in Text-fig. 8A; *i*3, *z*3, *J*3, *J*4, *Z*3, *px*2 and *px*3 lacking. Chaetotaxy of opisthonotal region variable. Most of the setae short and spinose. Surface of shield granular.

Tritosternum with base 48 μ, laciniae 132 μ. Sternal shield (150 $\mu \times$ 207 μ) with three pairs of setae and two pairs of pores. Metasternal setae on distinct shields. Between *st*1, 80 μ; between *st*1 and *st*3, 120 μ. Genital shield (174 $\mu \times$ 126 μ) flask-shaped, bearing four pairs of setae; between *gen.*, 105 μ; between *Jv*2, 99 μ. Anal shield (140 $\mu \times$ 93 μ) elongate pear-shaped, with paranal setae situated posterior to the anus. Paranals 18 μ long, postanal seta 57 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 8B. Peritreme extends to middle of coxa I. Peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs normal except genu III, which lacks seta *pv* (2—$\frac{2}{1}$, $\frac{2}{0}$—1) and genu IV, which has two postero-lateral setae (2—$\frac{2}{1}$, $\frac{3}{0}$—2). Both setae on coxa I and posterior setae on coxae II–III stout and spine-like; coxa II with well-developed anterior spine. Many of the leg setae stout and spinose. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	96/82	90/78	57/63	80/54
tibia	72/60	63/63	51/54	82/48
tarsus	90/48	105/50	105/45	147/42

Male: Chelicera with segment I, 40 μ; II, 66 μ; movable digit 48 μ long, partially fused with spermadactyl. Fixed digit greatly reduced, bearing an elongate pilus dentilis; both digits edentate (Text-fig. 9G). Four pairs of gnathosomal setae with *c.s.* about 57 μ apart; *hyp.*2 about 48 μ apart. Corniculi 30 μ long; other gnathosomal structures as in female.

Dorsal shield (612 $\mu \times$ 360 μ) with 32 pairs of setae distriuted as in Text-fig. 8C, the setae being relatively longer and more slender than in the female. Unsclerotized integument of dorsum bears seven to eight pairs of setae, one pair at the posterior margin and six to seven pairs on the mid-lateral margin.

Tritosternum with base 33 μ, laciniae 66 μ. Holoventral shield (528 $\mu \times$ 168 μ) with nine pairs of setae, excluding the anals. Between *st*1, 57 μ; between *st*1 and *st*3, 117 μ. Paranal setae 12 μ long, postanal seta at least three times this length. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 8D. Peritreme extends to middle of coxa I; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs as in female. Stout, spine-like coxal setae relatively longer and more slender than in female. Tarsus IV of male with three stout, spur-like setae (Text-fig. 9B). Length/width (in μ) of leg segments:

	I	II	III	IV
genu	90/75	75/75	60/63	90/60
tibia	72/60	54/60	50/54	88/54
tarsus	90/42	93/42	93/42	135/40

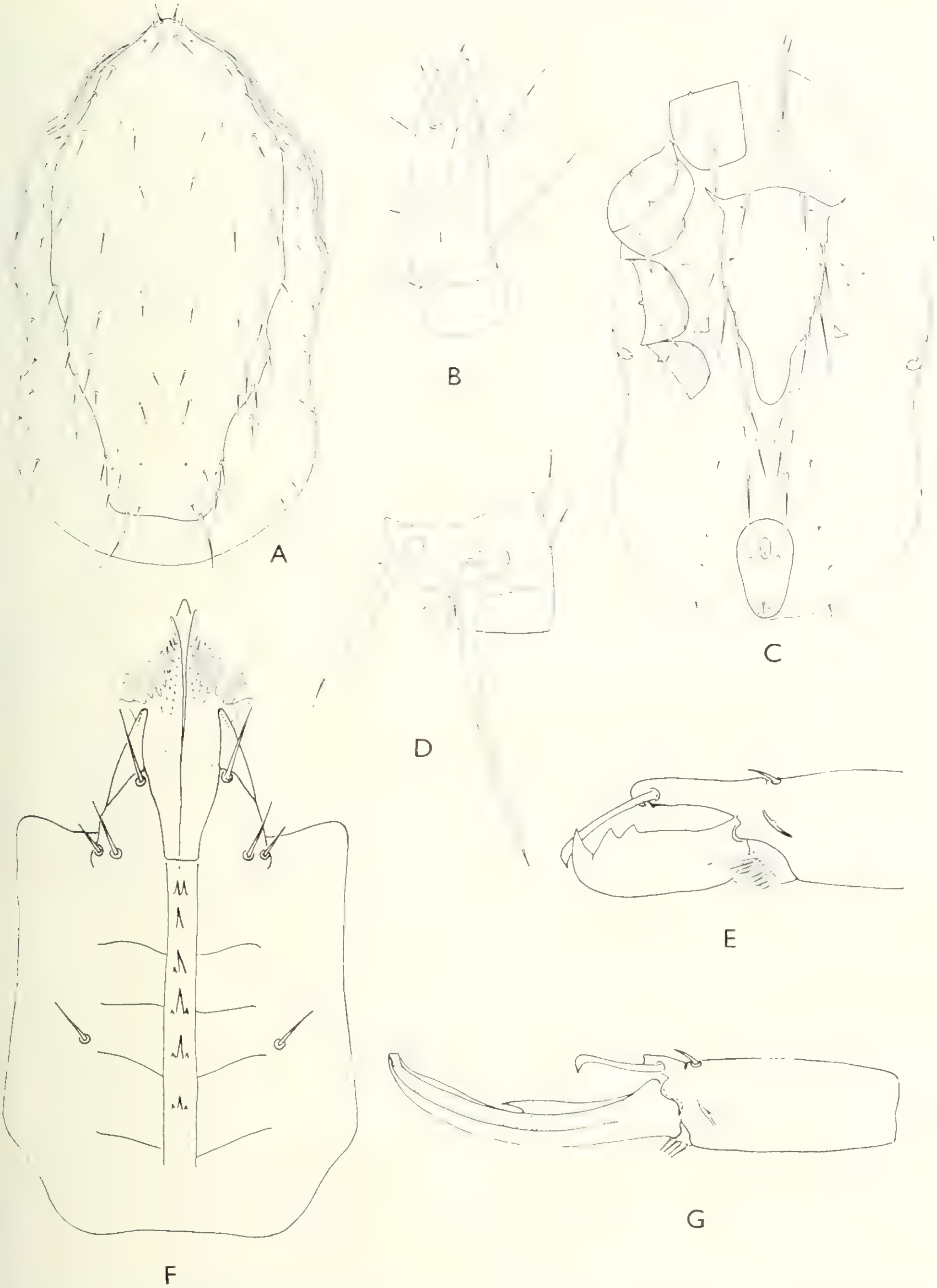

Fig. 9. *Ondatralaelaps multispinosa* (Banks). A. Dorsum of idiosoma of deutonymph (male); B. tarsus IV of male; C. venter of idiosoma of deutonymph (male); D. femur I of male, dorsal view; E. chelicera of female; F. venter of gnathosoma of female; G. chelicera of male.

Deutonymph (*male*) : Chelicera with segment I, 36 μ ; II, 80 μ ; chelae as in female, movable digit 27 μ. Four pairs of gnathosomal setae with *c.s.* about 54 μ apart ; *hyp.*2 about 45 μ apart. Gnathosomal structures generally as in female.

Dorsal shield (540 μ × 228 μ) with 16 pairs of setae in the podonotal region, 11–12 pairs in the opisthonotal region (Text-fig. 9A).

Tritosternum with base 42 μ, laciniae 100 μ ; Sternal shield (240 μ × 117 μ) with four pairs of setae and three pairs of pores. Between *st*1, 60 μ ; between *st*1 and *st*3, 110 μ. Anal shield (96 μ × 66 μ) ; par- and postanal setae very short, about 8 μ and 10 μ long respectively. Opisthogastric cuticle with seven pairs of setae (Text-fig. 9C). Peritreme extends to middle of coxa I ; peritrematal shields free anteriorly, poorly developed posteriorly.

Chaetotaxy of legs as in female, but setae not so markedly enlarged. Length width (in μ) of leg segments :

	I	II	III	IV
genu	78/72	66/66	45/57	63/50
tibia	63/58	50/57	45/50	63/45
tarsus	90/45	84/40	96/40	120/36

Deutonymph (*female*) : Slightly larger than male deutonymph and with eleven pairs of setae on the opisthogastric cuticle. Chelicera with segment I, 45 μ ; II, 96 μ ; movable digit 36 μ. Dorsal shield (588 μ × 240 μ) ; sternal shield (252 μ × 126 μ) ; anal shield (96 μ × 75 μ).

HABITAT : The musk rat, *Ondatra zibethica* (Linn.) in North America, Britain and Germany.

Genus ***ANDROLAELAPS*** Berlese

Androlaelaps Berlese, 1903, *Zool. Anz.* **27** : 14.
Haemolaelaps Berlese, 1910, *Redia* **6** : 216 ; and 1916, *Redia* **12** : 170.
Atricholaelaps Ewing, 1929, *Manual of External Parasites* : 186.
Eubrachylaelaps Ewing, 1929, *Manual of External Parasites* : 186.
Ischnolaelaps Fonseca, 1936, *Mem. Inst. Butantan S. Paulo* **10** : 19.
Cyclolaelaps Ewing 1933, *Proc. U.S. nat. Mus.* **82** (art. 30) : 5.
Turkiella Zumpt & Till, 1953, *An. Inst. Med. trop. Lisboa* **10** : 215.
Zygolaelaps Tipton, 1957, *J. Parasit.* **43** : 367.

Type : *Laelaps* (*Iphis*) *hermaphrodita* Berlese, 1887.

Medium sclerotized mites ranging from about 400 μ to 1,600 μ in length. Chelicerae usually chelate-dentate in the female with the movable digit bidentate ; occasionally this digit is edentate except for a terminal hook, and may have an additional cutting process with outwardly directed teeth. Fixed digit in the male markedly reduced, edentate ; movable digit usually edentate and partially fused with the elongated, grooved spermadactyl. Dorsal seta and fissures normal. Arthrodial processes present at base of movable digit. Chaetotaxy of venter of gnathosoma and pedipalps normal, apotele two-tined. Deutosternum with 6 rows of denticles, each row with from one to six denticles. Corniculi usually horn-like, occasionally reduced ; internal malae fringed or fimbriated. Tectum capituli membranous, rounded anteriorly, never denticulate.

Dorsal shield entire, usually with the basic 39 pairs of simple or barbed setae. This number may be increased by the addition of a pair of setae on the podonotal region (anterior accessory—*ax*) and/or a pair of setae (posterior accessory—*px*) on the opisthonotal region, giving patterns with 40 and 41 pairs of setae respectively. There may also be varying degrees of hypertrichy ranging from a few accessory setae between the *J* series to a dense covering of setae which completely obscures the basic pattern. The basic number of setae may be reduced by the absence of *z*3 or the *px* series, or one or more pairs of marginal setae may be situated on the unsclerotized integument.

Tritosternum normal, bipartite. No definite pre-endopodal shields. Sternal shield in the female with three pairs of setae and two pairs of pores. Genital shield narrow or variously inflated, bearing one pair of setae. Anal shield pear-shaped or subtriangular with normal setation. Opisthogastric cuticle with variable number of setae. Peritrematal shields free posteriorly. Metapodal shields present. Male usually with holoventral shield not fused with peritrematal shield; bearing from seven to ten pairs of setae, excluding the anals. A few species have a sternito-genito-ventral shield and a separate anal shield. Podal shields poorly developed posterior to coxae IV.

Chaetotaxy of legs normal except genu IV which has two postero-laterals ($2-\frac{2}{1}, \frac{3}{0}-2$). In some ethiopian species deviant patterns are found on tibia I ($2-\frac{3}{2}, \frac{3}{2}-2$), genu III ($2-\frac{2}{1}, \frac{2}{1}-2$) and tibia III ($2-\frac{1}{1}, \frac{2}{1}-2$) and in one species genu IV is normal. Seta av_1 on femur II may be modified to form a stout, spur-like structure in both sexes, or in the male only, of certain species. Ambulacra of all legs with paired claws. Coxa II has a small anterior spine.

KEY TO MALES AND FEMALES

1 Both sexes with pilus dentilis inflated basally, distal portion slender, curved (Text-fig. 12B). Greatest width of genital shield in female at the level of the first pair (*Zv*1) of opisthogastric setae (Text-fig. 12C) . ***A. fahrenholzi*** (Berlese) (p. 156)

– Both sexes with pilus dentilis slender, setiform (Text-fig. 10D). Greatest width of genital shield in female approximately at level of second pair (*Jv*1) of opisthogastric setae (Text-fig. 10B) . . . . ***A. casalis*** (Berlese) s. lat.

2 Dorsal shield 620 μ–710 μ long in female, 466 μ–485 μ long in male ; seta *Z*5 slender, setiform, about one and one-half times as long as *J*5 (Text-fig. 11B). Associated with birds and rodents . . . . ***A. casalis*** s. str. (p. 152)

– Dorsal shield 504 μ long in female, 402 μ long in male ; seta *Z*5 stout, subspiniform, scarcely longer than *J*5 (Text-fig. 11C). Associated with ants ***A. casalis myrmecophila*** ssp. nov. (p. 154)

Androlaelaps casalis casalis (Berlese)

?*Gamasus fenilis* Mégnin, 1876[4], *J. Anat. Physiol. Paris* **12** : 332.
Iphis casalis Berlese, 1887, *Acari, Myr. Scorp. Ital* fasc. 38, no. 8, figs. 3–5.
Androlaelaps casalis : Till, 1963, *Bull. Brit. Mus.* (*nat. Hist.*) *Zool.* **10** : 23, figs. 6–9, 25–29.
Hypoaspis oculatus Oudemans, 1915, *Arch. Naturgesch.* (A) **81** : 134.
Hypoaspis soarianus Hull, 1925, *Ann. Mag. nat. Hist.* (9), **15** : 209 (**syn. nov.**).
Haemolaelaps molestus Oudemans, 1929, *Ent. Ber. Amst.* **8** : 13.
Atricholaelaps megaventralis Strandtmann, 1947, *Proc. ent. Soc. Wash.* **49** : 112.
Hypoaspis freemani Hughes, 1948, *Mites associated with stored food products* : 129, figs. 173–179.
Haemolaelaps haemorrhagicus Asanuma, 1952, *Misc. Rep. Res. Inst. Nat. Res.* no. 25 : 87, fig. 1.

Female : Chelicera with segment I, 63 μ ; II, 108 μ ; movable digit 36 μ, bidentate ; fixed digit with two or three teeth ; pilus dentilis slender, setiform (Text-fig. 10D). Four pairs of gnathosomal setae with *c.s.* about 60 μ apart ; *hyp.2* about 42 μ apart. Deutosternum with six transverse rows of denticles (2–6 per row). Corniculi 36 μ long, internal malae fringed. Tectum capituli with smooth anterior margin. Salivary styli conspicuous, not reaching tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (620–710 μ × 376–429 μ) with the normal 39 pairs of simple setae and a variable number of unpaired accessory setae distributed as in Text-fig. 10A. Surface of shield reticulate ; two pairs of *r* and seven pairs of *R* setae on the cuticle.

Tritosternum with base 54 μ, laciniae 80 μ. Sternal shield (100 μ × 126 μ) with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between *st1*, 80 μ ; between *st1* and *st3*, 96 μ. Genital shield (177 μ × 105 μ) flask-shaped with one pair of setae. Anal shield (90 μ × 102 μ) with par- and postanal setae about 42 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 10B. Peritreme extends to middle of coxa I ; peritrematal shield free posteriorly ; anterior tip almost touches, but is not fused with, dorsal shield.

Chaetotaxy of legs differs from normal pattern in having two posterolateral setae on genu IV. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	87/38	72/45	54/36	78/33
tibia	90/33	70/42	57/33	80/33
tarsus	147/30	120/30	120/30	162/27

Male : Chelicera with segment I, 40 μ ; II, 75 μ ; movable digit 40 μ, 54 μ with spermadactyl ; both digits edentate (Text-fig. 10E). Four pairs of gnathosomal setae with *c.s.* about 48 μ apart ; *hyp.2* about 33 μ apart. Corniculi 27 μ long ; deutosternum, internal malae, tectum and pedipalps as in female.

Dorsal shield (466–485 μ × 276–322 μ) with the usual 39 pairs of setae and three unpaired accessory setae. Surface of shield reticulated.

Tritosternum with base 33 μ, laciniae 66 μ. Holoventral shield (384 μ × 95 μ) with four pairs of setae and three pairs of pores in the sternal region, six pairs of setae

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[4] It is not possible to be certain of the identity of this species from its short and inadequate original description.

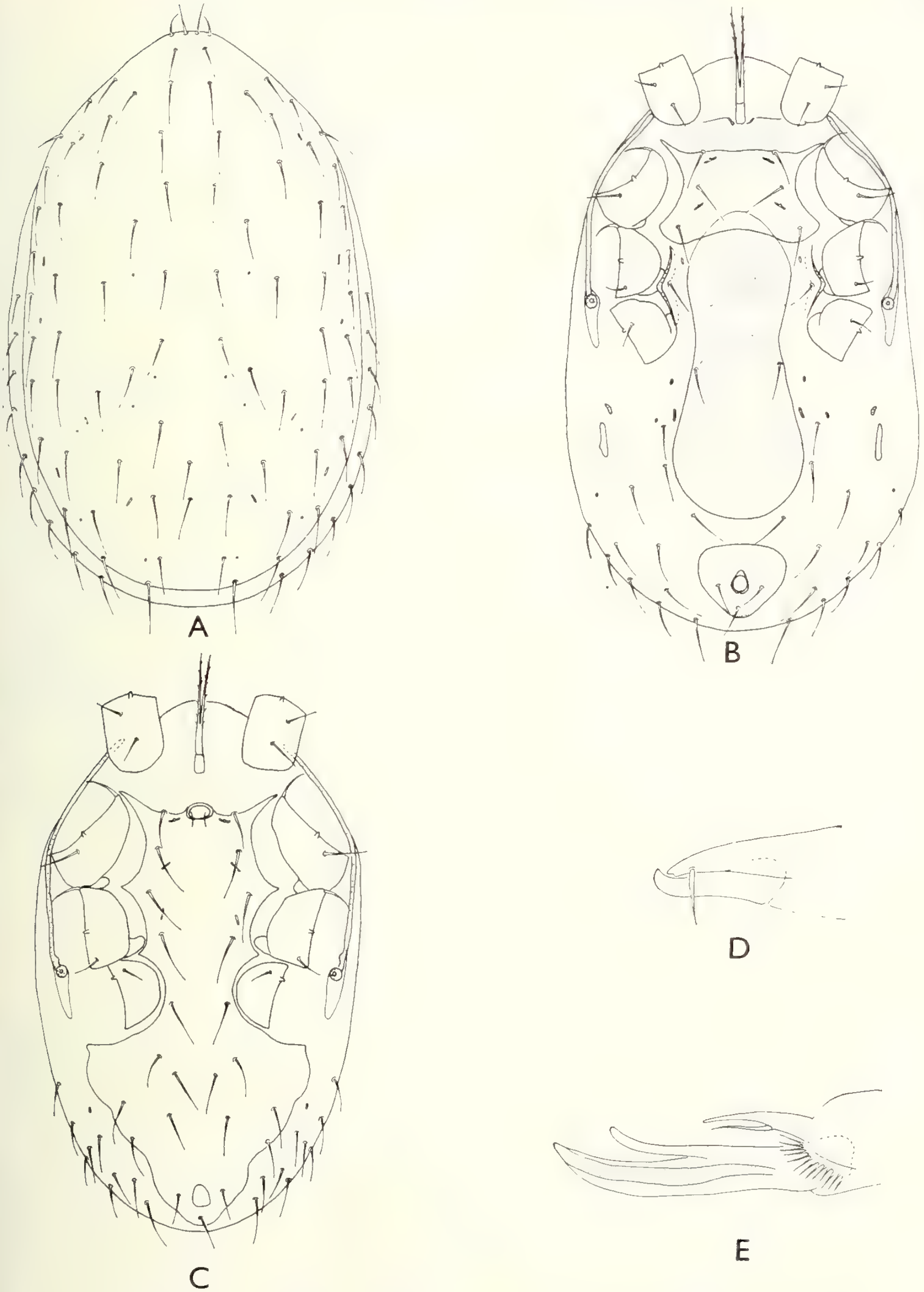

FIG. 10. *Androlaelaps casalis casalis* (Berlese). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. venter of idiosoma of male; D. chelicera of female; E. chelicera of male.

in the genito-ventral region. Between *st*1, 60 μ; between *st*1 and *st*3, 80 μ. Paranal setae 18 μ, postanal seta 27 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 10C. Peritreme extends to middle of coxa I; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	72/36	70/45	50/33	70/33
tibia	78/30	60/40	50/30	72/30
tarsus	120/28	87/30	87/27	130/24

HABITAT: Cosmopolitan, in the nests of birds, in poultry litter and also on rodents.

Androlaelaps casalis myrmecophila ssp. nov.

In all instars this subspecies closely resembles *Androlaelaps casalis* s. str. from which it differs in certain of its measurements and in having setae *Z*5 at the posterior margin of the dorsal shield relatively short and stout (Text-fig. 11C).

Female: Dorsal shield (504 μ × 288 μ) with the usual 39 pairs of setae and two to three unpaired accessory setae distributed as in Text-fig. 11A. Sternal shield (80 μ × 105 μ) not sharply demarkated from pre-sternal area. Between *st*1, 72 μ; between *st*1 and *st*3, 78 μ. Genital shield (140 μ × 84 μ) with genital setae only. Anal shield (72 μ × 72 μ) with par- and postanal setae subequal, about 30 μ long.

Chaetotaxy of legs as in *A. casalis* s. str. Tibia and tarsus II with relatively stout, spinose, ventral setae. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	70/32	54/36	42/27	63/27
tibia	75/27	50/36	45/27	66/27
tarsus	130/26	84/24	90/22	120/22

Male: Gnathosoma as in *A. casalis* s. str. Dorsal shield (402 μ × 222 μ) with chaetotaxy and setal form as in female. Holoventral shield (324 μ × 90 μ) expanded behind coxae IV, with ten pairs of setae excluding the anals. Between *st*1, 57 μ; between *st*1 and *st*3, 66 μ. Par- and postanal setae about 20 μ long.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	66/30	54/36	38/27	60/27
tibia	69/26	48/33	40/26	60/26
tarsus	110/24	75/24	75/21	108/21

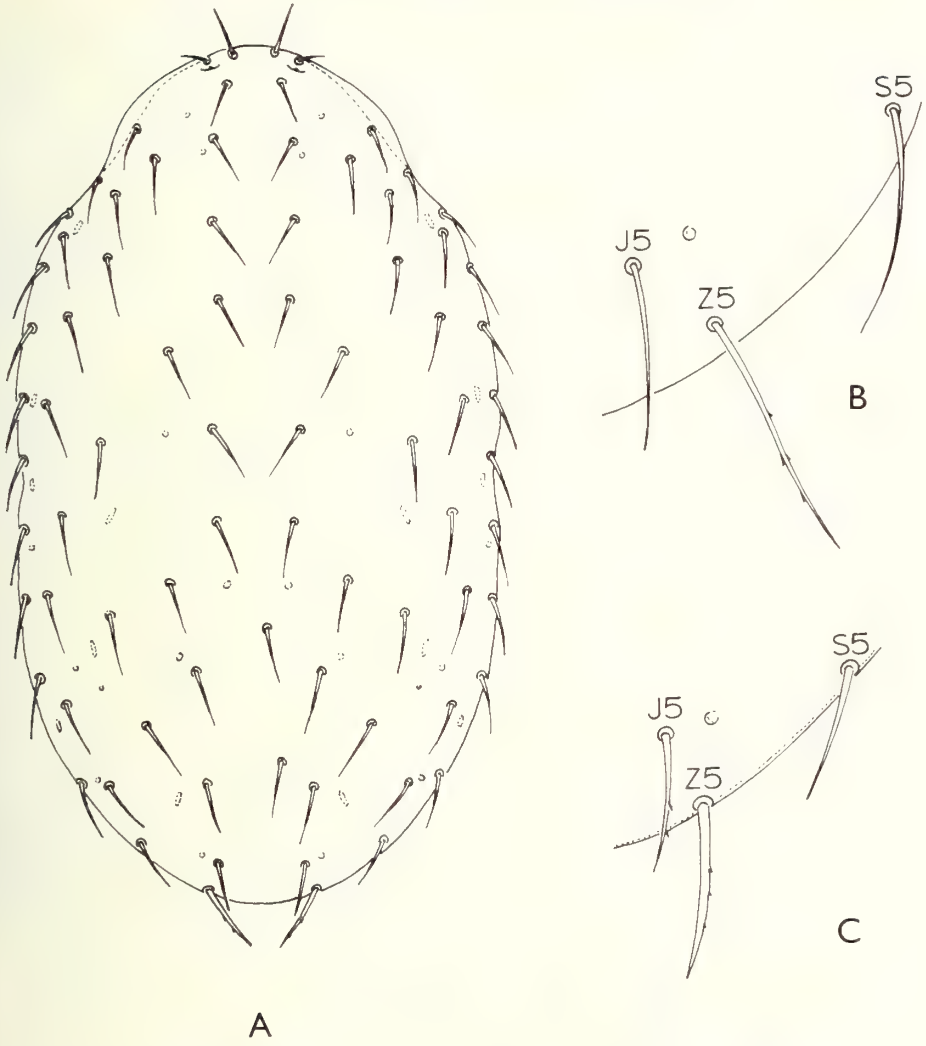

Fig. 11. A. *Androlaelaps casalis myrmecophila* ssp. nov.; dorsum of idiosoma of female. B–C. Relative lengths of dorsal setae *J*5, *Z*5, and *S*5 of *A. casalis casalis* (B) and *A. casalis myrmecophila* (C).

Protonymph: Chelicera with segment I, 36 μ; II, 66 μ; movable digit 22 μ. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp.*2 about 33 μ apart. Corniculi 27 μ long; pedipalp (1–4–5–12) with two-tined apotele.

Podonotal shield (210 μ × 186 μ) with eleven pairs of setae; pygidial shield (96 μ × 156 μ) with eight pairs of setae; mesonotal region with four pairs of scutellae.

Tritosternum with base 40 μ, laciniae 54 μ. Sternal shield (about 144 μ × 93 μ) with anterior margin indistinct. Between *st*1, 63 μ; between *st*1 and *st*3, 102 μ. Anal shield (48 μ × 60 μ) with par- and postanal setae about 24 μ long. Peritreme extends to middle of coxa III.

Chaetotaxy of legs normal. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	54/33	45/36	33/27	45/28
tibia	54/30	42/33	33/27	48/27
tarsus	93/26	63/24	69/24	93/22

Deutonymph : Chelicera with segment I, 40 μ ; II, 68–70 μ ; movable digit 21 μ. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.*2 about 30 μ apart. Corniculi 24 μ long ; other gnathosomal features as in female.

Dorsal shield (348 $\mu \times$ 198 μ) with lateral incisions and bearing the usual 39 pairs of setae and two or three accessories.

Tritosternum with base 40 μ, laciniae 54 μ. Sternal shield (about 174 $\mu \times$ 72 μ) with anterior margin indistinct ; bearing four pairs of setae and three pairs of pores. Between *st*1, 54 μ ; between *st*1 and *st*3, 78 μ. Anal shield (48 $\mu \times$ 45 μ ; maximum width 60 μ) ; par- and postanal setae about 20 μ long. Peritreme extends to posterior third of coxa I ; peritrematal shield weakly developed.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	54/30	45/34	30/27	48/27
tibia	57/26	42/30	33/24	48/24
tarsus	96/24	66/24	70/21	93/21

HABITAT : From the nests of *Formica rufa* Linn. Holotype ♀ (1965 : 12 : 29 : 7) and female paratype (1965 : 12 : 29 : 8) from the Black Wood of Rannoch, Perthshire (coll. R. M. Emberson, 13 April 1964) ; male allotype (1965 : 12 : 29 : 9), male and female paratypes (1965 : 12 : 29 : 10), protonymph and deutonymph from Ufton Park, Berkshire (coll. C. A. Collingwood). The specimens are deposited in the collection of the British Museum (Natural History), London.

Androlaelaps fahrenholzi (Berlese)

Laelaps (*Haemolaelaps*) *fahrenholzi* Berlese, 1911, *Redia* **7** : 432.
Liponyssus setiger Ewing, 1920, *Ent. News* **31** : 290, figs. 6–7.
Laelaps glasgowi Ewing, 1925, *Proc. ent. Soc. Wash.* **27** : 6.
Androlaelaps glasgowi : Till, 1963, *Bull. Brit. Mus.* (*nat. Hist.*) *Zool.* **10** : 40, figs. 65–68.
Laelaps californicus Ewing, 1925, *Proc. ent. Soc. Wash.* **27** : 5.
Laelaps virginianus Ewing, 1925, *Proc. ent. Soc. Wash.* **27** : 6.
Hypoaspis microti Oudemans, 1926, *Ent. Ber. Amst.* **7** : 101.
Haemolaelaps mohrae Oudemans, 1928, *Ent. Ber. Amst.* **7** : 374.
Haemolaelaps cricetophilus Vitzthum, 1930, *Zool. Jb. Jena, Abt. Syst.* **60** : 417.
Laelaps stegemani Hefley, 1935, *J. Kansas ent. Soc.* **8** : 22.
Ischnolaelaps rhabdomys Radford, 1939, *Parasitology* **31** : 249.
Haemolaelaps scalopi Keegan, 1946, *Trans. Amer. Micr. Soc.* **65** : 71.
Atricholaelaps sigmodoni Strandtmann, 1946, *J. Parasit.* **32** : 164.
Atricholaelaps strandtmanni Fox, 1947, *Ann. ent. Soc. Amer.* **40** : 580.
Hypoaspis (*Haemolaelaps*) *eos* Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* **14** : 79.

Female : Chelicera with segment I, 72 μ ; II, 126 μ ; movable digit 36 μ, bidentate ; fixed digit bidentate ; pilus dentilis inflated basally, distal portion slender, curved (Text-fig. 12B). Four pairs of gnathosomal setae with *c.s.* about 72 μ apart ; *hyp.*2 about 54 μ apart. Deutosternum with six transverse rows of denticles (3–5 per row) ; corniculi 30 μ long ; internal malae fringed. Tectum capituli with smooth anterior margin. Salivary styli slender, extending to tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (714 μ × 432 μ) with the normal 39 pairs of setae distributed as in Text-fig. 12A ; some anterior setae barbed. Surface of shield reticulated ; no hypertrichy in British specimens ; with two pairs of *r* and seven pairs of *R* setae on the cuticle.

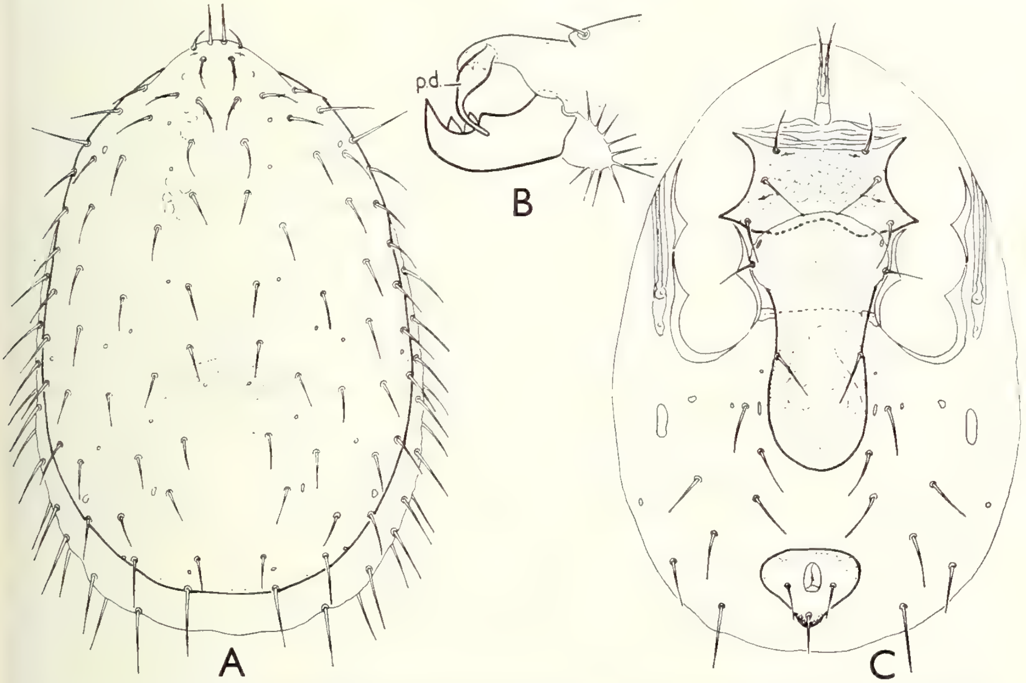

FIG. 12. *Androlaelaps fahrenholzi* (Berlese), female ; dorsum of idiosoma (A) ; chelicera (B) ; venter of idiosoma (C).

Tritosternum with base 45 μ, laciniae 135 μ. Sternal shield (96 μ × 168 μ) with three pairs of setae and two pairs of pores. Metasternals free with associated pores. Between *st*1, 96 μ ; between *st*1 and *st*3, 102 μ. Genital shield tongue-shaped (156 μ × 114 μ), with genital setae only. Anal shield (90 μ × 112 μ) with paranal setae 54 μ, postanal seta 66 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 12C. Peritreme extends to middle of coxa I ; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs differs from normal pattern in having two postero-lateral setae on genu IV. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	96/45	90/60	70/45	105/45
tibia	93/36	80/57	70/42	110/42
tarsus	162/36	126/42	144/36	240/36

Male: Described and figured by Till (1963).

HABITAT: Cosmopolitan, chiefly on rodents and in their nests. Also recorded from birds, bats and small carnivores.

Genus *HYPOASPIS* Canestrini

Hypoaspis Canestrini, 1884, *Atti. Ist. Veneto* (6) **2**: 1569; 1885, *Acarofauna ital.* part 1 : 55.

Type: *Gamasus krameri* Canestrini, 1881.

Chelicerae typically chelate-dentate with the movable digit bidentate in the female, rarely digits edentate or specialized for egg-feeding in certain myrmecophilous forms. Pilus dentilis normally short, setiform; dorsal seta and fissures present. Chelicerae of male chelate, movable digit usually unidentate, spermadactyl free, distally grooved and never completely fused with the movable digit. Arthrodial processes simple, rarely absent. Chaetotaxy of the venter of the gnathosoma and of the pedipalps normal, apotele two or three-tined, the latter with subequal tines. Deutosternum with six, rarely five, transverse rows of denticles. Corniculi horn-like, salivary styli present. Tectum capituli with anterior margin smooth or denticulate.

Entire dorsal shield typically with 39 pairs of setae, *px2* and *px3* being present. Variations in the basic pattern are the result of absence of *px2* and *px3* (37 pairs), *r2* and *r4* on lateral integument (37 pairs), *z3* and *r1* absent (37 pairs), presence of extra *r* seta (40 pairs) or extra *r* seta and *px* (41 pairs). Unpaired accessory setae in the region of the *J* series may be present or absent.

Tritosternum normal, bipartite. Pre-endopodal shields occasionally present. Sternal shield in the female usually with three pairs of setae and two pairs of pores; first pair of setae may be placed on the pre-sternal area (*Cosmolaelaps* group). Genital shield flask-shaped with one pair of setae, or, genito-ventral shield variously inflated and bearing one to three pairs of opisthogastric setae situated on its lateral margins. Anal shield usually pear-shaped or subtriangular, with normal chaetotaxy. Opisthogastric cuticle with variable number of setae. Peritrematal shields free posteriorly or fused with podal shields. Metapodal shields present. Male usually with holoventral shield which may or may not be fused with the peritrematal shields, and which bears 9 or 10 pairs of setae excluding the anals. Anal shield occasionally free. Podal shields poorly or well developed posterior to coxae IV.

Chaetotaxy of legs usually normal. Variations result from addition of seta pl_2 on tibia III (2—$\frac{1}{1}$, $\frac{2}{1}$—2), seta pl_2 or *pv* on genu IV (2—$\frac{2}{1}$, $\frac{3}{0}$—2 or 2—$\frac{2}{1}$, $\frac{3}{1}$—1) and the absence of al_2 on genu IV (1—$\frac{2}{1}$, $\frac{3}{0}$—1). Anterior spine on coxa II small or absent. Ambulacra usually with paired claws; claws on leg I occasionally reduced or absent. A ventral seta on femur II in the male, or both sexes, sometimes enlarged and spine-like.

The present classification of the *Hypoaspis* complex is largely based on palaearctic forms and requires radical revision. It appears to be well represented in the nearctic, tropical and subtropical regions and we feel that a knowledge of the extra-palaearctic forms is an essential prerequisite to any attempt at a " generic " classification of the complex. According to the current classification of *Hypoaspis*, the majority of the British species may be distributed among the following of its subgenera :

HYPOASPIS s. str. (type : *Gamasus krameri* G. & R. Canestrini, 1881).
  H. krameri (Canestrini).
ALLOPARASITUS Berlese, 1920 (type: *Laelaps* (*Hypoaspis*) *oblongus* Halbt., 1915) syn: *Halbertia*, Hull in Turk & Turk, 1952.
  H. oblonga (Halbt).
COSMOLAELAPS Berlese, 1903 (type : *Laelaps claviger* Berlese, 1883).
  H. claviger (Berlese) ; *H. cuneifer* (Michael) ; *H. vacua* (Michael) ; *H. neocuneifer* sp. nov.
GAEOLAELAPS Trägårdh, 1952 (type : *Laelaps aculeifer* Canestrini, 1884).
  H. aculeifer (Canestrini) ; *H. giffordi* sp. nov.; *H. lubrica* Voigts & Oudemans ;
  H. praesternalis Willmann and (?) *H. sardoa* Berlese.
GYMNOLAELAPS Berlese, 1903 (type : *Laelaps myrmecophilus* Berlese, 1892).
  H. myrmecophila (Berlese) ; *H. laevis* (Michael) and
  H. myrmophila (Michael).
HOLOSTASPIS Kolenati, 1858 (type : *Holostaspis isotricha* Kolenati, 1858).
  H. isotricha Kolenati ; *H. montana* (Berlese) and *H. oophila* (Wasman).
LAELASPIS Berlese, 1903 (type : *Iphis astronomicus* Koch, 1839).
  H. astronomica (Koch) ; *H. humerata* (Berlese) and *H. equitans* (Michael).
PNEUMOLAELAPS Berlese, 1920 (type : *Iphis bombicolens* Canestrini, 1885).
  H. bombicolens (Canestrini) ; *H. marginalis* Willmann ;
  H. breviseta sp. nov. ; *H. colomboi* sp. nov. ; *H. hyatti* sp. nov. and *H. minutissima* sp. nov.
STRATIOLAELAPS Berlese, 1916 (type : *Laelaps* (*Iphis*) *miles* Berlese, 1882).
  syn. *Davisiella* Zumpt & Patterson, 1951 (**syn. nov.**)
  H. miles (Berlese).
Hypoaspis heselhausi Oudms. and *H. nidicorva* sp. nov., and *H. acuta* (Michael) appear to represent distinct species-groups.

There is little doubt that certain of these subgenera represent natural bio-morphological groups, although the boundaries between them cannot be satisfactorily defined on the basis of their morphological characteristics alone, even in such apparently distinct groups as *Pneumolaelaps*, *Holostaspis* and *Gymnolaelaps*.[5] In view of this we are disregarding the subgeneric divisions in the following key to the British species of the complex.

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[5] There are, at present, no comprehensive definitions or keys to the subgenera of *Hypoaspis*. The placing of species within the subgenera has largely been by rule of thumb, generally following Berlese's (1903) concepts. The following key, based on eco-morphological characteristics provides a guide to the subgenera or species-groups represented in the British fauna.

(*Footnote continued on p.* 160)

Key to Females

1 Genu IV with eight setae, an antero-lateral seta lacking $(1\text{—}\frac{2}{1}, \frac{3}{0}\text{—}1)$; peritrematal shields free posteriorly and extending well beyond posterior margins of coxae IV (Text-fig 46F) . . . . **_H. oblonga_** (Halbt.) (p. 222)

– Genu IV with 9 or 10 setae, two antero-lateral setae present $(2\text{—}\frac{2}{1}, \frac{3}{0}\text{—}1$; $2\text{—}\frac{2}{1}, \frac{3}{1}\text{—}1$ or $2\text{—}\frac{2}{1}, \frac{3}{0}\text{—}2)$; peritrematal shield not extending posterior to coxae IV, free or fused with the podal shields 2

2 Dorsal shield lacking setae *px* on the opisthonotal region and never with unpaired accessory setae ; dorsal setae leaf-like, spatulate (Text-fig. 45A) ; corniculi long, slender, extending almost to the level of the anterior margin of the palpfemur **_H. miles_** (Berlese) (p. 222)

– Dorsal shield with setae *px* present, with or without unpaired accessory setae; dorsal setae various ; corniculi relatively shorter, if reaching beyond the level of the middle of the palpfemur then dorsal setae simple 3

(*Footnote continued from p.* 159)

1 Genu IV with eight setae $(1\text{—}\frac{2}{1}, \frac{3}{0}\text{—}1)$; peritrematal shield in the female free posteriorly and extending well beyond the posterior margins of coxae IV (Text-fig. 46F) **_Alloparasitus_** Berlese

– Genu IV with nine or ten setae ; peritrematal shield in the female not extending posterior to coxae IV, free or fused with podal shields 2

2 Dorsal shield lacking setae *px* in the opisthonotal region and never with unpaired accessory setae ; dorsal setae leaf-like, spatulate. Corniculi long, slender, extending almost to the level of the anterior margin of the palpfemur **_Stratiolaelaps_** Berlese

– Dorsal shield with setae *px* present, with or without unpaired accessories ; dorsal setae various. Corniculi relatively shorter, if reaching to the middle of the palpfemur then dorsal setae simple 3

3 Dorsal setae spatulate, cuneiform or scimitar-like. Free-living or myrmecophilous **_Cosmolaelaps_** Berlese

– Dorsal setae simple or pilose, never markedly flattened 4

4 Certain setae of the dorsum and of the segments of the legs (femur II, femur and tarsus IV) long and whip-like. Associated with Coleoptera **_Hypoaspis_** s. str.

– Setae of the dorsum rarely, and legs never, long and whip-like 5

5 Genu IV with two ventral setae $(2\text{—}\frac{2}{1}, \frac{3}{1}\text{—}1)$; peritremes usually broad ; lateral and ventral cuticle often densely setose. In nests of *Bombus* **_Pneumolaelaps_** Berlese

– Genu IV with one ventral seta $(2\text{—}\frac{2}{1}, \frac{3}{0}\text{—}1/2)$, if with two ventral setae, then peritremes narrow 6

6 Apotele with three subequal tines. Discrete, well-sclerotized pre-endopodal shields present ; dorsal shield with 40–41 pairs of setae (excluding unpaired accessories). Myrmecophilous **_Gymnolaelaps_** Berlese

– Apotele two-tined. Usually without discrete pre-endopodal shields ; dorsal shield with not more than 39 pairs of setae (excluding unpaired accessories) 7

7 Digits of the chelicerae in the female stumpy, dentate or edentate and modified for oophagy, movable digit about 20 μ in length. Myrmecophilous **_Holostaspis_** Kolenati

– Digits of the chelicerae in the female normal in form, dentate or edentate ; movable digit at least 35 μ in length 8

8 Genito-ventral shield in the female markedly inflated posterior to coxae IV, flanked by linear metapodals and characteristically ornamented. Dorsal setae long, whip-like, or marginal setae serrated. Myrmecophilous or free-living **_Laelaspis_** Berlese

– Genital or genito-ventral shield otherwise ; dorsal setae never long or whip-like. Free-living or inhabitants of nests of birds and mammals **_Gaeolaelaps_** Trägårdh (including **_heselhausi-nidicorva_** group)

3 Dorsal setae *j2–3*, *z2–4*, *S4–5* and *Z4* considerably longer than other dorsal setae, *Z4* very long and whip-like (Text-fig. 13A) ; seta pd_1 on femur II, ad_1 on femur IV, ad_{2-3} and pd_2 on tarsus IV long and whip-like. Associated with *Lucanus* (Coleoptera) . . . . . . **H. krameri** (Canestrini) (p. 163)

– Dorsal chaetotaxy otherwise ; leg setae never long and whip-like 4

4 Dorsal setae spatulate (Text-fig. 24C), cuneiform (Text-fig. 25C) or scimitar-like (Text-fig. 28A–C) 5

– Dorsal setae simple or pilose, never markedly flattened 8

5 Majority of dorsal setae cuneiform (Text-fig. 25C) 6

– Majority of dorsal setae spatulate or scimitar-like 7

6 Genu IV with two postero-lateral setae (2—$\frac{2}{1}$, $\frac{3}{0}$—2) ; dorsal seta *S2* clavate, considerably shorter than cuneiform seta *S1* (Text-fig. 25A) ; proximal region of cuneiform seta only slightly enlarged (Text-fig. 25C) . **H. cuneifer** (Michael) (p. 184)

– Genu IV with one postero-lateral seta (2—$\frac{2}{1}$, $\frac{3}{0}$—1) ; dorsal setae *S1–2* cuneiform, subequal (Text-fig. 26A) ; proximal region of cuneiform seta conspicuously enlarged (Text-fig. 26D) . . . . **H. neocuneifer** sp. nov. (p. 187)

7 Dorsal setae spatulate, clavate (Text-fig. 24C) ; peritremes extending to the level of the vertical setae (*j1*) ; sternal shield with strong reticulate pattern (Text-fig. 24D) **H. claviger** (Berlese) (p. 182)

– Dorsal setae scimitar-like (Text-fig. 28A–C) ; peritremes extending to the level of the middle of coxae I ; sternal shield without conspicuous ornamentation (Text-fig. 27B) . . . . **H. vacua** (Michael) (p. 190)

8 Genu IV with two ventral setae, *pv* present (2—$\frac{2}{1}$, $\frac{3}{1}$—1) 9

– Genu IV with one ventral seta, *pv* absent (2—$\frac{2}{1}$, $\frac{3}{0}$—1 or 2—$\frac{2}{1}$, $\frac{3}{0}$—2) 16

9 Capitular setae and setae on coxae I–II stout, spinelike. Associated with *Bombus* (Hymenoptera) . . . . . . **H fuscicolens** (Oudemans) (p. 196)

– Capitular setae and setae on coxae I–II slender, normal 10

10 Dorsal shield shows hypertrichy between the *J* series ; surface of shield with a clearly defined reticulate pattern 11

– Dorsal shield without hypertichy between the *J* series ; surface of shield with or without a distinct reticulate pattern 14

11 Sternal shield distinctly wider than long (L/W = 0·7) ; deutosternum with six rows each consisting of 2–8 unequally sized denticles. 12

– Sternal shield about as wide as long (L/W = 1·0) or longer than wide (L/W = 1·1) ; deutosternum with six rows each of at least six small, uniform, denticles. . . 13

12 Opisthogaster densely setose, region between genital and anal shields with about twenty setae (Text-fig. 34B) ; ratio of distance between genital setae to the maximum width of the genital shield about 1·15 **H. marginalis** (Willmann) (p. 199)

– Opisthogaster not densely setose, region between genital and anal shields with four setae (Text-fig. 33B) ; ratio of distance between genital setae to maximum width of genital shield about 1·3 . . . . . . **H. hyatti** sp. nov. (p. 198)

13 Dorsal shield about 700 μ in length ; setae *j2* extending at least three-quarters of the distance between *j2* and *j3* ; setae on distal third of tarsus II distinctly thickened, spine-like. Associated with nests of birds and small mammals **H. lubrica** Voigts & Oudemans (p. 172)

– Dorsal shield about 500 μ in length ; setae *j2* extending to about one-half the distance between *j2* and *j3* ; setae on distal third of tarsus II not distinctly thickened nor spine-like. Associated with *Bombus* . . **H. minutissima** sp. nov. (p. 201)

14 Sternal shield longer than wide (L/W = 1·1). Opisthogastric setae subequal in length. Peritreme relatively narrow ; length of posterior part of peritrematal shield at least three times the width of the peritreme (Text-fig. 31B) **H. colomboi** sp. nov. (p. 194)

– Sternal shield wider than long (L/W = 0·6). Opisthogastric setae flanking genital shield about twice as long as those near the margin of the body. Peritreme relatively wide ; length of posterior part of peritrematal shield not more than twice the width of the peritreme 15

15 Setae on anterior part of dorsal shield relatively long ; seta *j3* reaches base of seta *j4* (Text-fig. 29A) ; surface of shield with distinct reticulate pattern in addition to sculptured areas for muscle attachment . . ***H. bombicolens*** (Canestrini) (p. 191)

– Setae on anterior part of dorsal shield relatively short ; seta *j3* extends about half-way to base of seta *j4* ; surface of shield without a distinct reticulate pattern ***H. breviseta*** sp. nov. (p. 193)

16 Genu IV with two postero-lateral setae ($2-\frac{2}{1}, \frac{3}{0}-2$) (Text-fig. 44C) 17

– Genu IV with one postero-lateral seta ($2-\frac{2}{1}, \frac{3}{0}-1$) (Text-fig. 44B) 19

17 Antero-ventral seta on femur II and genu II stout and spine-like (Text-fig. 20D) ; tibia III with two postero-lateral setae ($2-\frac{1}{1}, \frac{2}{1}-2$) ; dorsal shield with 39 pairs of setae (Text-fig. 20A) . . . . ***H. sardoa*** Berlese (p. 175)

– Antero-ventral seta on femur II and genu II not conspicuously thickened ; tibia III with one postero-lateral seta ($2-\frac{1}{1}, \frac{2}{1}-1$) ; dorsal shield with 37 or 41 pairs of setae. Myrmecophilous 18

18 Dorsal shield about 1,100 μ in length with 41 pairs of short, fine, dorsal setae (Text-fig. 43D) ; apotele with three subequal tines . . ***H. laevis*** (Michael) (p. 220) –

– Dorsal shield about 700 μ in length with 37 pairs of medium, relatively stout, dorsal setae (Text-fig. 41A) ; apotele with two subequal tines ***H. acuta*** (Michael) (p. 212) –

19 Peritrematal shield fused with the expodal shield in the region of coxa IV. . . . 20

– Peritrematal shield free posteriorly 21

20 Dorsal setae short, setae *J1* reaching about mid-way between the bases of *J1* and *J2* (Text-fig. 21A) ; genito-ventral shield sub-rectangular in outline (Text-fig. 21D) with a pair of setae lying between the genito-ventral and anal shields ***H. heselhausi*** (Oudemans) (p. 177)

– Dorsal setae long, seta *J1* reaching beyond the bases of *J2* by about one-half their length (Text-fig. 22A) ; genito-ventral shield flask-shaped (Text-fig. 22B), without setae between the genito-ventral and anal shields . ***H. nidicorva*** sp. nov. (p. 179)

21 Apotele with three subequal tines (Text-fig. 42C) 22

– Apotele with two subequal tines. 23

22 Larger species, over 1,000 μ ; sternal shield with L/W = 0·8 ; genito-ventral shield as in Text-fig. 42B . . . . . . ***H. myrmecophila*** (Berlese) (p. 214)

– Smaller species, about 700 μ ; sternal shield almost twice as broad as long (L/W = 0·5) ; genito-ventral shield as in Text-fig. 43B . ***H. myrmophila*** (Michael) (p. 218)

23 Dorsum with only one pair of setae in the *R* series (Text-fig. 19A) ; peritreme extending to about the middle of coxa II (Text-fig. 19E) ; Small species about 500 μ in length . . . . ***H. praesternalis*** Willmann (p. 173)

– Dorsum with five or more pairs of setae in the *R* series ; peritreme extending up to or beyond coxa I 24

24 Majority of dorsal and opisthogastric setae very long, sinuous (Text-figs. 40 A and E) ; setae *J3* extending beyond the bases of setae *J4* by at least a quarter of their length. Myrmecophilous 25

– Dorsal and opisthogastric setae normal in length ; setae *J3* never reach the bases of *J4* 26

25 Legs relatively short and stumpy ; leg IV (trochanter to tarsus) about one-half the length of the dorsal shield ; movable digit of the chelicera strongly bidentate (Text-fig. 40D). . . . . ***H. humerata*** Berlese (p. 212)

– Legs relatively long and slender ; leg IV (trochanter to tarsus) scarcely shorter than the dorsal shield ; movable digit of chelicera edentate (Text-fig. 40B) ***H. equitans*** (Michael) (p. 210)

26 Femur II with antero-ventral seta stout, spine-like ; tarsus IV with long, stout, spine-like setae ; genital shield small . . . ***H. aculeifer*** (Canestrini) (p. 166)

– Femur II with antero-ventral seta simple, not conspicuously thickened ; tarsus IV without long spine-like setae 27

27 Cheliceral digits normal, slender ; movable digit longer than the palpfemur and strongly bidentate 28

– Cheliceral digits atypical, stumpy ; movable digit shorter than the palpfemur, weakly dentate or edentate 29

28 Genito-ventral shield greatly expanded posterior to coxae IV ; metapodal shields flanking genito-ventral shield ; marginal setae of dorsal shield strong, serrated ***H. astronomica*** (Koch) (p. 208)

– Genital shield relatively narrow posterior to coxae IV ; metapodal shields widely removed from its margins (Text-fig. 17E) ; dorsal setae simple ***H. giffordi*** sp. nov. (p. 170)

29 Dorsal setae of the *J* series markedly unequal in length ; setae *J*4 and *J*5 pilose distally and considerably longer and stouter than simple setae *J*1–*J*3 (Text-fig. 38A). Myrmecophilous . . . . ***H. oophila*** (Wasman) (p. 207)

– Dorsal setae of the *J* series subequal in length 30

30 Dorsal seta *Z*5 pilose distally and about three times the length of simple seta *J*5 (Text-fig. 37A) ; movable digit of the chelicera edentate (Text-fig. 37B) ***H. montana*** (Berlese) (p. 206)

– Dorsal seta *Z*5 less than twice the length of seta *J*5 (Text-fig. 36A) ; movable digit of the chelicera dentate (Text-fig. 36D) . . . ***H. isotricha*** (Kolenati) (p. 203)

Hypoaspis krameri (Canestrini)

Gamasus krameri Canestrini G. & R., 1881, *Atti Ist. Veneto* (5) **7** : 1083, figs.

Female : Chelicera with segment I, 72 μ ; II, 180 μ ; movable digit 80 μ, bidentate ; fixed digit with about ten teeth (Text-fig. 13D) ; pilus dentilis short, setiform ; dorsal seta about twice as long as the pilus. Four pairs of gnathosomal setae with *c.s.* about 72 μ apart, *hyp.*2 about 60 μ apart. Deutosternum with six transverse rows of denticles (6–7 per row) ; corniculi 66 μ ; internal malae as in Text-fig. 13C. Tectum capituli with anterior margin denticulate (Text-fig. 13B). Salivary stylus extends nearly to tip of corniculus. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (684 μ × 396 μ) with 37 pairs of setae distributed as in Text-fig. 13A ; seta *s*3, the humeral seta and seven pairs of marginal setae on the cuticle. Setae *j*2–3, *z*2–6, considerably longer than the other setae, seta *Z*4 extremely long and sinuous ; no hypertrichy. Surface of shield granular.

Tritosternum with base 45 μ, laciniae 123 μ. Sternal shield (117 μ × 150 μ) with three pairs of setae and three pairs of pores, the third pair being on the posterior margin of the shield ; metasternal setae free. Between *st*1, 93 μ ; between *st*1 and *st*3, 114 μ. Genital shield (114 μ × 105 μ) with genital setae only. Anal shield (93 μ × 72 μ) with paranal setae 48 μ, postanal seta 30 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 13F. Peritreme extends beyond middle of coxa I ; peritrematal shields free anteriorly and posteriorly.

Legs with normal chaetotaxy. Long, whip-like setae present on femur II (pd_1), femur IV (ad_1) and tarsus IV (ad_2 and pd_{2-3}), Text-fig. 14A. Tarsus II with two

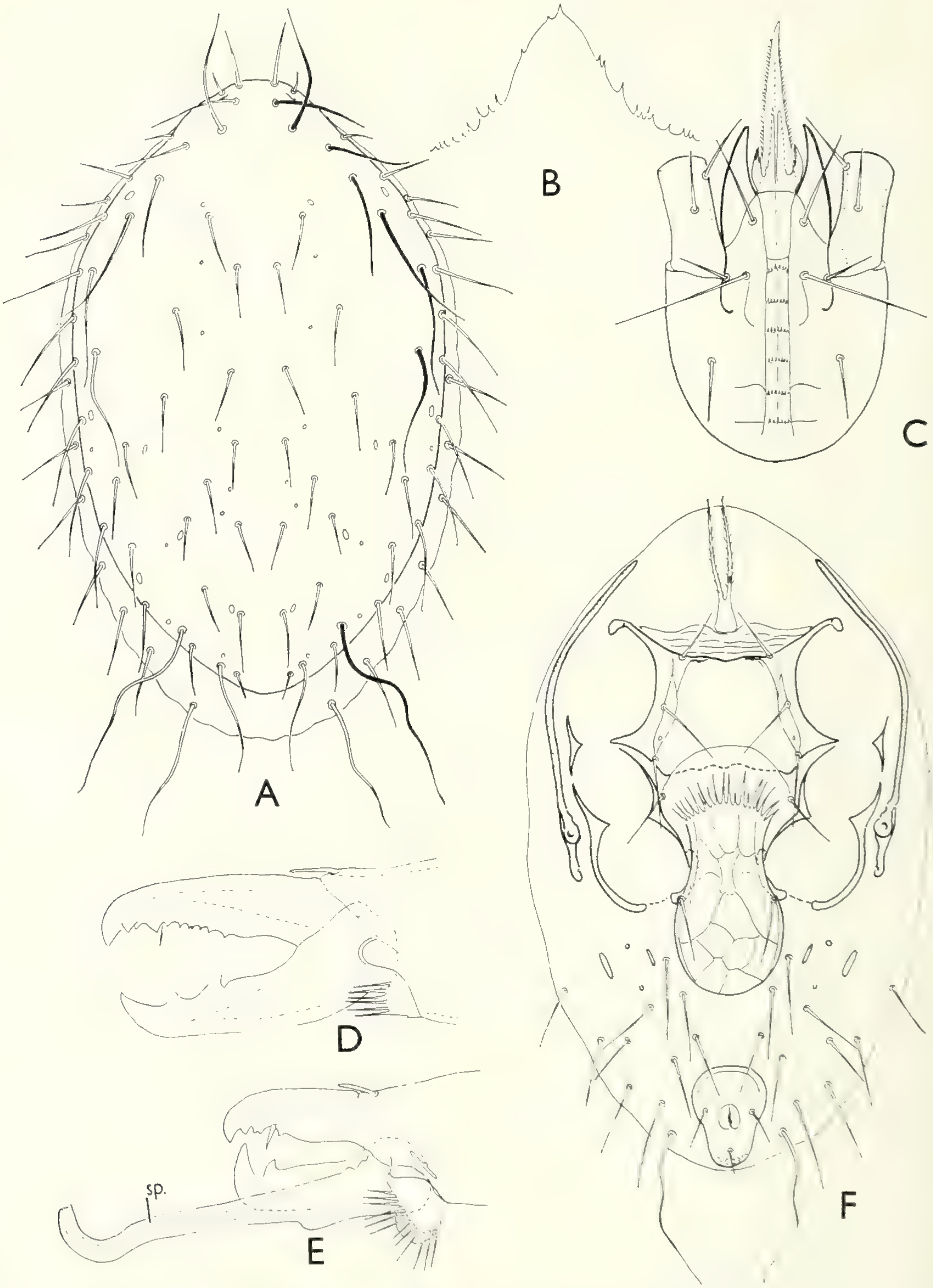


Fig. 13. *Hypoaspis krameri* (Canestrini). A. Dorsum of idiosoma of female; B. tectum capituli of female; C. venter of gnathosoma of female; D. chelicera of female; E. chelicera of male; F. venter of idiosoma of female.

stout, blunt setae (al_1 and pl_1) and several which are stout basally, tapering to fine points (av_{1-2}, pv_{1-2}, mv) ; relatively thick setae on tibia II (av_1 and pv_1) and genu II (av). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	93/42	84/57	66/45	90/45
tibia	108/33	84/54	75/42	100/45
tarsus	140/33	120/42	144/36	190/36

Male : Chelicera with segment I, 72 μ ; II, 168 μ ; movable digit 70 μ, unidentate ; spermadactyl 130 μ long, slender (Text-fig. 13E) ; fixed digit tridentate ; pilus dentilis and dorsal seta as in female. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 50 μ apart. Details of gnathosomal structure not clearly visible.

Dorsal shield (636 $\mu \times 348$ μ) as in female. Tritosternum with base 45 μ, laciniae 114 μ. Holoventral shield (516 $\mu \times 114$ μ) with four pairs of setae in the sternal region, six pairs in the genito-ventral region ; moderately expanded behind coxae IV but not extending beyond lateral margins of the coxae. Between *st*1, 80 μ ; between *st*1 and *st*3, 123 μ. Peritreme extends beyond middle of coxa I.

Legs with normal chaetotaxy ; long whip-like setae on legs II and IV as in female. Leg II (Text-fig. 14B) bears several stout setae : $a\ v_1$ and especially $a\ v_2$ on the femur ;

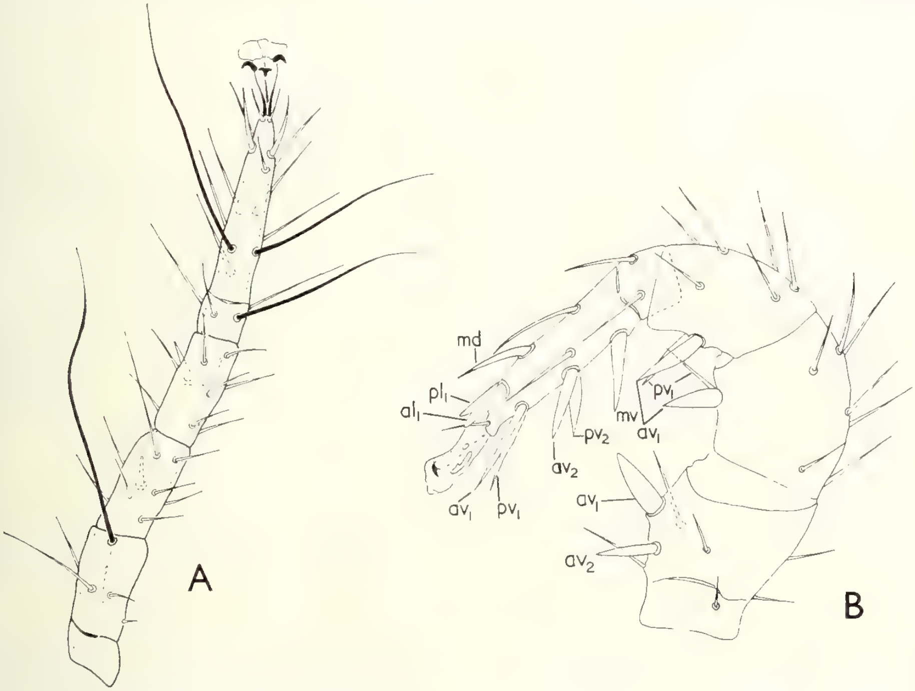


FIG. 14. *Hypoaspis krameri* (Canestrini). A. Leg IV of female ; B. leg II of male.

av on the genu ; *av* and *pv* on the tibia ; al_1, pl_1, av_2, pv_2, *mv* on the tarsus ; setae av_1, pv_1 and *md* on the tarsus are fairly stout basally, tapering to fine points. Legs all bent and not suitable for measurement.

HABITAT : Recorded from *Lucanus* sp. (Coleoptera) in Britain and from *Oryctes nasicornis* Linn. in the Netherlands.

Hypoaspis aculeifer (Canestrini)

Laelaps aculeifer Canestrini, 1884, *Atti Ist. Veneto* (6) **2** : 698.
Hypoaspis aculeifer: Bregetova, 1956, *Opred. Faune SSSR.* **61** : 77, figs. 102–106.

Female : Chelicera with segment I, 75 μ ; II, 216 μ ; movable digit 98 μ, bidentate ; fixed digit with about 10 teeth (Text-fig. 15B) ; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 66 μ apart and *hyp.2* about 50 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 60 μ long ; internal malae fringed (Text-fig. 15D). Tectum capituli with denticulate anterior margin (Text-fig. 15F). Salivary styli conspicuous. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (684 μ × 360 μ) with normal 39 pairs of simple setae distributed as in Text-fig. 15A. Setae of podonotal region conspicuously longer than those on the opisthonotal region. Surface of shield reticulate ; no hypertrichy ; with seven pairs of *R* setae on the cuticle.

Tritosternum with base 48 μ, laciniae 105 μ. Sternal shield (190 μ × 138 μ) extending almost to posterior margin of coxa III, with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between *st*1, 75 μ ; between *st*1 and *st*3, 144 μ. Genital shield flask-shaped (120 μ × 96 μ) with one pair of setae. Anal shield (90 μ × 75 μ), with paranal seta 27 μ and postanal seta 36 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 15C. Peritreme extends to middle of coxa I ; peritrematal shields free posteriorly, anterior region fused with dorsal shield at level of *r*1.

Legs with normal chaetotaxy. Tarsus II with setae av_{1-2}, pv_{1-2}, al_1, pl_1, *md*, *mv*, ad_2, stout and spine-like. Tibia II with *av* and *pv* stout ; genu II with *av* stout ; femur II with av_1 stout. Stout setae are found on genu III (*av* and *pv*), tibia III (*av* and *pv*), tarsus III (most setae, except al_2, pl_2, ad_3, pd_3), genu IV (*av*), tibia IV (av_1, pv_1, pl_1) and tarsus IV (most setae). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	96/40	105/66	63/50	105/63
tibia	114/30	96/66	66/48	120/63
tarsus	180/28	135/48	156/40	240/48

Male : Chelicera with segment I, 54 μ ; II, 130 μ ; movable digit 60 μ, unidentate, spermadactyl as in Text-fig. 15G ; fixed digit with about 5 teeth ; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.2*

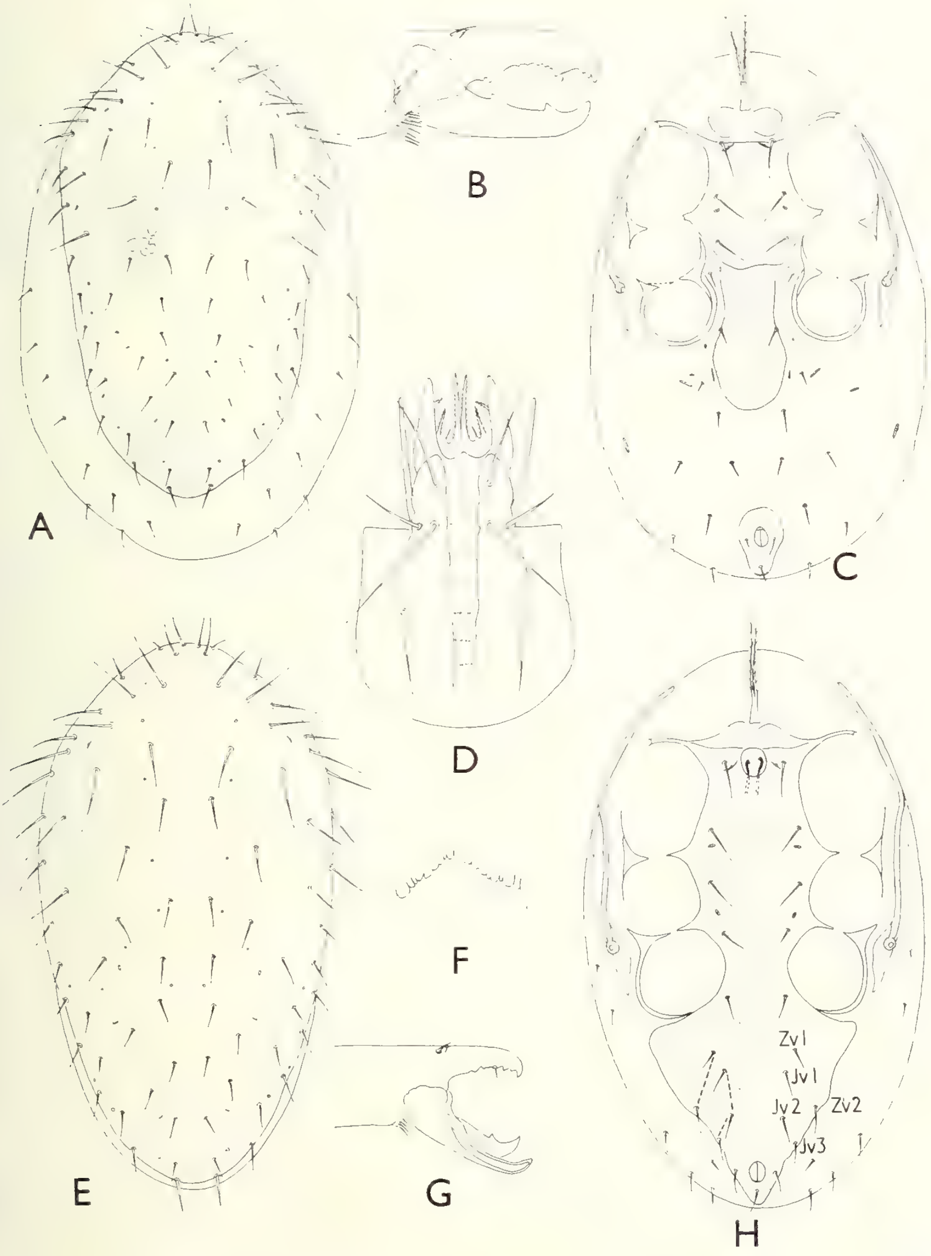


FIG. 15. *Hypoaspis aculeifer* (Canestrini). A. Dorsum of idiosoma of female ; B. chelicera of female ; C. venter of idiosoma of female ; D. venter of gnathosoma of female ; E. dorsum of idiosoma of male ; F. tectum capituli of female ; G. chelicera of male ; H. venter of idiosoma of male.

about 42 μ apart. Deutosternum, internal malae, tectum capituli as in female; corniculi 54 μ long. Pedipalps as in female.

Dorsal shield (540 μ × 276 μ) with 39 pairs of setae distributed as in Text-fig. 15E. Tritosternum with base 27 μ, laciniae 78 μ. Holoventral shield (456 μ × 114 μ) with three pairs of sternal, one pair of metasternal setae and three pairs of pores in the sternal region; between *st*1, 63 μ; between *st*1 and *st*3, 126 μ. Genito-ventral region with six pairs of setae. Paranal setae about 24 μ, postanal seta about 20 μ long. Chaetotaxy of opisthogaster as in Text-fig. 15H. Peritreme extends nearly to middle of coxa I; anterior part of peritrematal shield fused with dorsal shield; posterior part free.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	75/33	80/54	50/42	84/54
tibia	90/27	75/54	50/40	90/54
tarsus	150/24	110/40	130/36	186/45

Protonymph: Chelicera with segment I, 40 μ; II, 132 μ; movable digit 50 μ. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp*.2 about 36 μ apart. Deutosternum, internal malae and tectum as in female; corniculi 36 μ long. Pedipalp (1–4–5–12) with two-tined apotele.

Podonotal shield (258 μ × 190 μ) with eleven pairs of setae; pygidial shield (90 μ × 120 μ) with eight pairs of setae; chaetotaxy and sclerotization of mesonotal region as in Text-fig. 16A.

Tritosternum with base 30 μ, laciniae 60 μ. Sternal shield (170 μ × 80 μ) with three pairs of setae and two pairs of pores; between *st*1, about 48 μ; between *st*1 and *st*3, about 120 μ. Anal shield (50 μ × 42 μ) with paranal setae 20 μ and postanal seta 18 μ long. Chaetotaxy of opisthogaster as in Text-fig. 16 B. Peritreme extends to middle of coxa III.

Legs with normal chaetotaxy. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	60/30	60/36	40/30	57/33
tibia	66/30	50/40	42/30	60/36
tarsus	114/27	78/33	87/27	130/33

Deutonymph: Chelicera with segment I, 40 μ; II, 147 μ; movable digit 57 μ. Deutosternum, hypostomal processes, corniculi and tectum as in protonymph. Pedipalp (2–5–6–14) as in female.

Dorsal shield (450 μ × 216 μ) with lateral incisions, bearing 39 pairs of setae arranged as in Text-fig. 16C; no hypertrichy; with seven pairs of *R* setae on the cuticle.

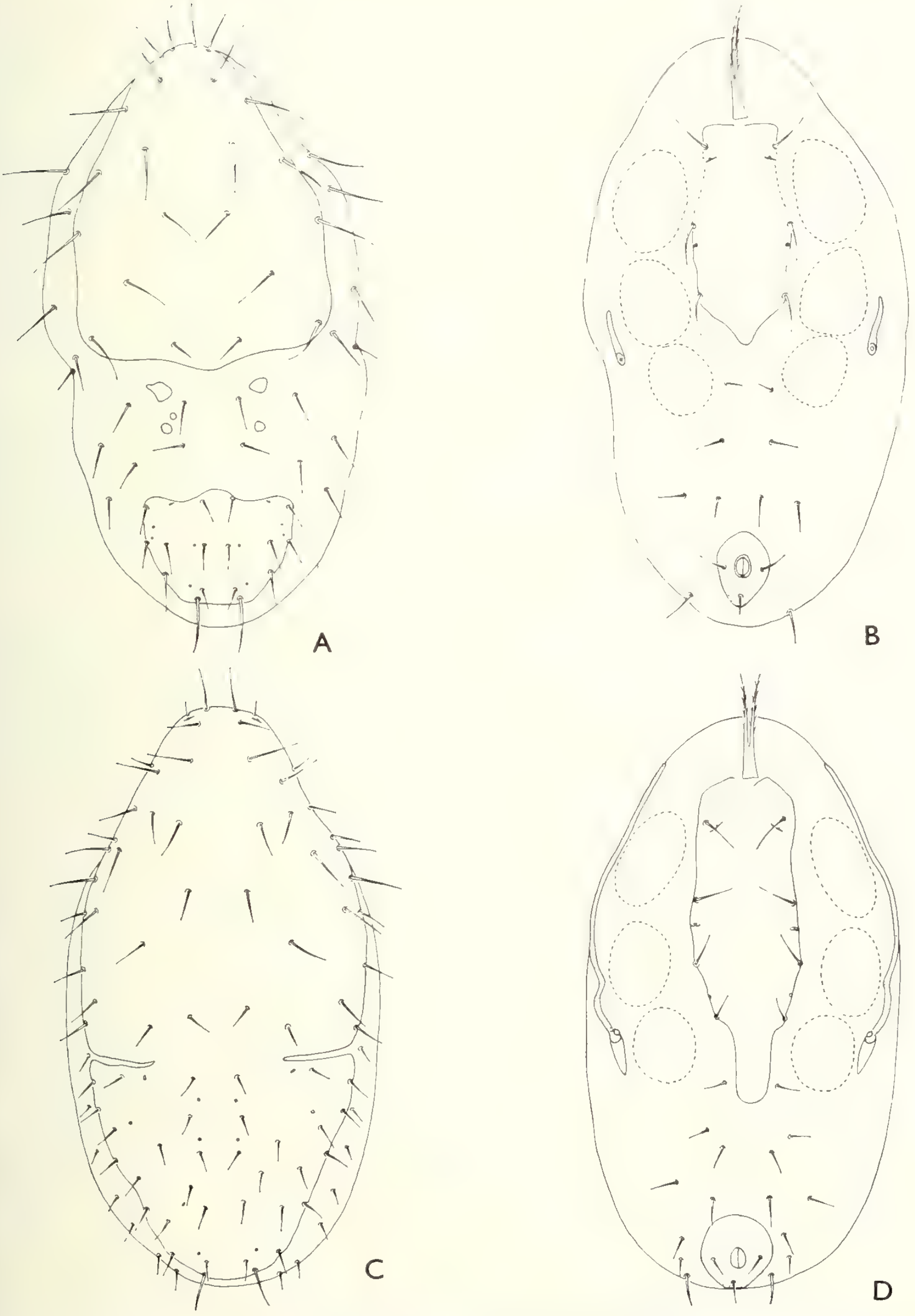


FIG. 16. *Hypoaspis aculeifer* (Canestrini). A. Dorsum of idiosoma of protonymph; B. venter of idiosoma of protonymph; C. dorsum of idiosoma of deutonymph; D. venter of idiosoma of deutonymph.

Tritosternum with base 40 μ, laciniae 65 μ. Sternal shield (243 $\mu \times$ 82 μ) bears three pairs of sternal, one pair of metasternal setae and three pairs of pores ; between *st*1, 60 μ ; between *st*1 and *st*3, 114 μ. Anal shield (approximately 57 $\mu \times$ 50 μ) with par- and postanal setae about 18 μ long. Chaetotaxy of opisthogaster as in Text-fig. 16D. Peritreme as in female.

Chaetotaxy of legs normal. Tibia IV with av_1, pv_1 and pl_1 stout. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	66/33	72/48	48/42	60/42
tibia	78/30	57/48	48/40	72/50
tarsus	123/24	96/30	102/30	135/36

HABITAT : Common in soil and litter. Recorded from the nest of *Riparia riparia* (Linn.) in Gloucestershire, Britain ; from the nest of *Spalax ehrenbergi* Nehring in Israel and the nests of a variety of rodents in the U.S.S.R.

Hypoaspis giffordi sp. nov.

Female : Chelicera with segment I, 45 μ ; II, 120 μ ; movable digit 45 μ, bidentate ; fixed digit with three small teeth, pilus dentilis short, setiform (Text-fig. 17D). Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with six transverse rows of denticles (3–7 per row) ; corniculi 36 μ long ; internal malae reduced (Text-fig. 17B). Tectum capituli with anterior margin smooth (Text-fig. 17C). Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (480 $\mu \times$ 276 μ) with 39 pairs of setae and four accessory setae distributed as in Text-fig. 17A. Surface of shield reticulate.

Tritosternum with base 24 μ, laciniae 54 μ. Sternal shield (100 $\mu \times$ 84 μ) weakly reticulate anteriorly and laterally, with three pairs of setae and two pairs of pores. Metasternal setae free with associated pores. Between *st*1, 60 μ ; between *st*1 and *st*3, 90 μ. Genital shield (84 $\mu \times$ 93 μ) with genital setae only. Anal shield (60 $\mu \times$ 72 μ) with paranal and postanal setae about 20 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 17E. Peritreme extends to middle of coxa I ; anterior tip of peritrematal shield fused with dorsal shield ; posterior part free.

Chaetotaxy of legs normal except in one specimen in which genu IV has a posteroventral seta on one side only. Tarsus II with ventral setae, al_1, pl_1 and *md* stouter than the other setae ; tarsus IV with seta pl_2 spine-like. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	63/30	54/36	40/28	60/28
tibia	70/27	48/33	36/28	60/28
tarsus	110/24	80/24	82/42	117/24

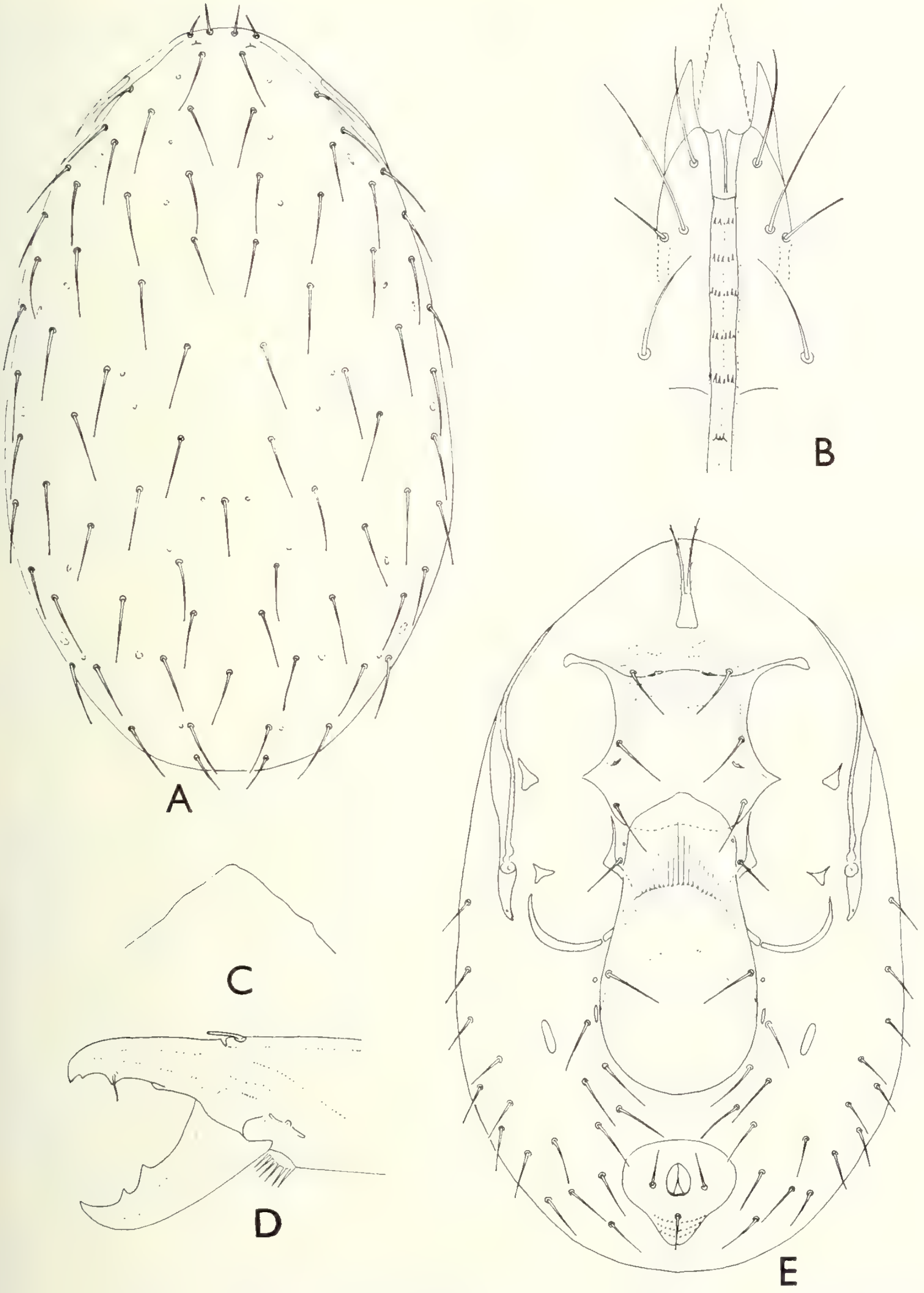


Fig. 17. *Hypoaspis giffordi* sp. nov., female ; dorsum of idiosoma (A) ; deutosternum and hypostome (B) ; tectum capituli (C) ; chelicera (D) ; venter of idiosoma (E).

HABITAT: Found on birch timber rotted by *Polyporus betulinus*, Rannoch, Perthshire. Collected by D. R. Gifford, November, 1962. Holotype ♀ (1965 : 12 : 29 : 3), paratype ♀ (1965 : 12 : 29 : 4).

Hypoaspis lubrica Voigts & Oudemans

Hypoaspis lubrica Voigts & Oudemans, 1904, *Zool. Anz.* **27** : 654.
Samsinak, 1960, *Acta Soc. ent. Čech.* **57** : 278, fig. 2 (1–9).
Hypoaspis (*Haemolaelaps*) *inversus* Berlese, 1918, *Redia* **13** : 127.
Hypoaspis compressus Hull, 1925, *Ann. Mag. nat. Hist.* (9) **15** : 209 (**syn. nov.**)
Hypoaspis smithii Hughes, 1948, *Mites associated with stored food products* : 131.
Hypoaspis murinus Strandtmann & Menzies, 1948 (1949), *Ann. ent. Soc. Amer.* **41** : 479, figs.

Female : Chelicera with segment I, 66 μ ; II, 156 μ ; movable digit 56 μ, bidentate, fixed digit tridentate ; pilus dentilis short, setiform (Text-fig. 18B). Four pairs of gnathosomal setae with *c.s.* about 66 μ apart ; *hyp.*2 about 42 μ apart. Deutosternum with six transverse rows of denticles (7–10 per row) ; corniculi 45 μ long ; internal malae fringed. Tectum capituli with fine striations and a smooth anterior margin (Text-fig. 18C). Salivary stylus reaches tip of corniculus. Pedipalp (2–5–6–14) with two-tined apotele.

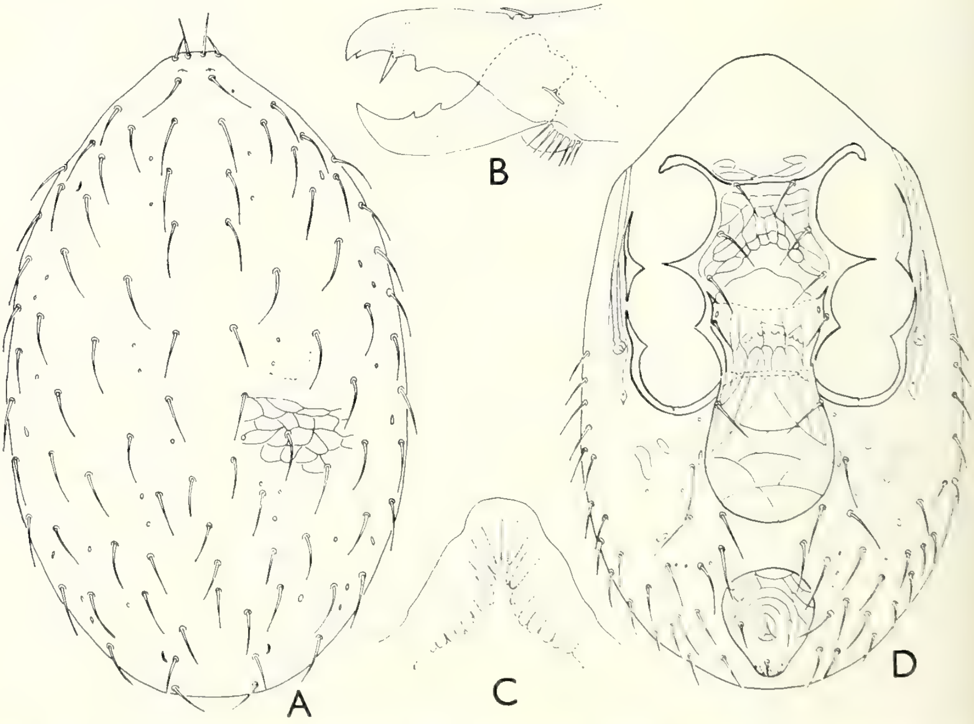


FIG. 18. *Hypoaspis lubrica* Voigts and Oudemans, female ; dorsum of idiosoma (A) ; chelicera (B) ; tectum capituli (C) ; venter of idiosoma (D).

Dorsal shield (708 μ × 420 μ) with 39 pairs of setae and 4–9 accessory setae distributed as in Text-fig. 18A. Surface of shield reticulated.

Tritosternum with base 30 μ, laciniae 90 μ. Sternal shield (132 μ × 120 μ) extending to middle of coxa III, with three pairs of setae and two pairs of pores; metasternal setae free with associated pores. Between *st*1, 70 μ; between *st*1 and *st*3, 112 μ. Genital shield (150 μ × 117 μ) flask-shaped with one pair of setae. Anal shield (110 μ × 105 μ) with par- and postanal setae 36 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 18D. Peritreme extends to beyond middle of coxa I; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs differs from typical pattern in having a postero-ventral seta on genu IV. Setae av_1, pv_1, al_1, pl_1 on tarsus II are stout and spine-like; setae av_2, pv_2 and *mv* are stout and pointed. Tibia II has stout ventral setae (av_1 and pv_1). Legs III and IV bear many stout ventral setae on the genu, tibia and tarsus. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	87/38	84/50	54/40	90/42
tibia	96/36	75/48	57/40	90/40
tarsus	147/33	105/36	130/33	174/33

HABITAT: In decaying oats and hay; in the nest of *Riparia riparia* (Linn.); on a variety of rodents and in their nests. Recorded from Britain, Europe, the U.S.S.R. and the U.S.A.

Hypoaspis praesternalis Willmann

Hypoaspis praesternalis Willmann, 1949, *Veröff. Mus. Nat. Bremen* no. 1A: 115, figs.
Hypoaspis nolli Karg, 1962, *Mitt. zool. Mus. Berlin* **38**: 62, figs. (**syn. nov.**).

Female: Chelicera with segment I, 50 μ; II, 144 μ; movable digit 60 μ, bidentate; fixed digit with bifid tip and four teeth, pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp*.2 about 42 μ apart. Deutosternum with six transverse rows of fine denticles; corniculi 52 μ long; internal malae slender, triangular, fringed. Tectum capituli with anterior margin denticulate (Text-fig. 19C). Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (492 μ × 264 μ) with 39 pairs of setae distributed as in Text-fig. 19A. No hypertrichy. Surface of shield reticulate. Two pairs of *R* setae on the cuticle.

Tritosternum with base 36 μ, laciniae 84 μ; presternal area reticulate and granular. Sternal shield (138 μ × 105 μ) with reticulate pattern most pronounced laterally; with three pairs of setae and two pairs of pores; metasternal setae free with associated pores. Between *st*1, 75 μ; between *st*1 and *st*3, 100 μ. Genital shield (90 μ × 72 μ) with genital setae only. Anal shield (72 μ × 70 μ) with paranal and postanal setae about 33 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 19E.

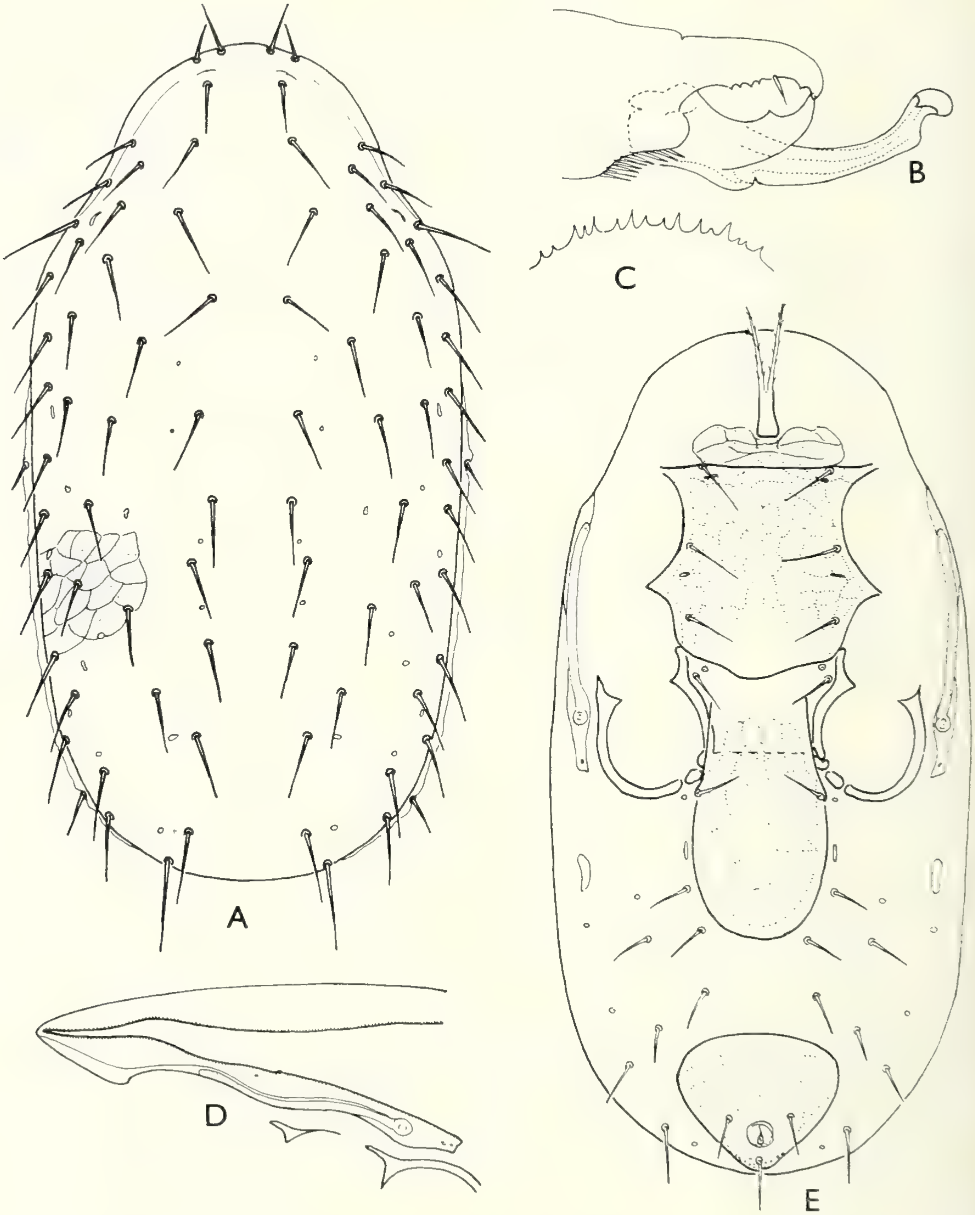


FIG. 19. *Hypoaspis praesternalis* Willmann. A. Dorsum of idiosoma of female; B. chelicera of male; C. tectum capituli of female; D. peritreme and peritrematal shield of female; E. venter of idiosoma of female.

Peritreme extends to about middle of coxa II ; anterior part of peritrematal shield fused with dorsal shield, posterior part free (Text-fig. 19D).

Chaetotaxy of legs normal. Tarsi II–IV with ventral setae relatively stout basally, tapering to long, fine points. Tarsus IV with setae pl_2 and pl_3 relatively stout and blade-like. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	68/30	60/36	40/27	63/30
tibia	75/24	54/36	40/27	66/32
tarsus	130/20	80/30	72/24	117/27

Male : Chelicera with segment I, 40 μ ; II, 105 μ ; movable digit 42 μ, unidentate ; fixed digit with bifid tip and four teeth, pilus dentilis simple ; spermadactyl large as in Text-fig. 19B. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp*.2 about 36 μ apart. Corniculi 36 μ long and set wider apart than in the female. Tectum and pedipalps as in female.

Dorsal shield (420 μ × 228 μ) with chaetotaxy similar to that in the female except for the absence of setae *px*2 in the opisthonotal region. Surface of shield reticulated.

Tritosternum with base 15 μ, laciniae 70μ. Holoventral shield (348 μ × 93 μ) with four pairs of setae and three pairs of pores in the sternal region, five pairs in the genito-ventral region ; anal region with normal three setae. Between *st*1, 66 μ ; between *st*1 and *st*3, 90 μ. Par- and post-anal setae subequal in length. Peritreme extends to about the middle of coxa II ; peritrematal shield free posteriorly.

Chaetotaxy of legs as in female. Setae of femur II simple. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	66/27	54/36	36/30	57/33
tibia	68/24	48/33	36/27	60/30
tarsus	117/20	72/27	70/24	105/26

HABITAT : Recorded from soil, grassland and marshes in Britain and Europe.

Hypoaspis sardoa (Berlese)

Laelaps (*Androlaelaps*) *sardous* Berlese, 1911, *Redia* **7** : 433.
Bregetova, 1956, *Opred. Faune SSSR.* **61** : 83, figs. 120–122.
Hypoaspis laevis var. pilifer Oudemans, 1912, *Ent. Ber. Amst.* **3** : 231.

Female : Chelicera with segment I, 102 μ ; II, 228 μ ; movable digit 90 μ, bidentate ; fixed digit with three teeth and a row of serrations ; pilus dentilis short, setiform (Text-fig. 20C). Four pairs of gnathosomal setae with *c.s.* about 68 μ apart, *hyp*.2 about 57 μ apart. Deutosternum with six transverse rows of denticles (4–8 per row) ; corniculi 90 μ long ; internal malae fringed (Text-fig. 20E). Tectum

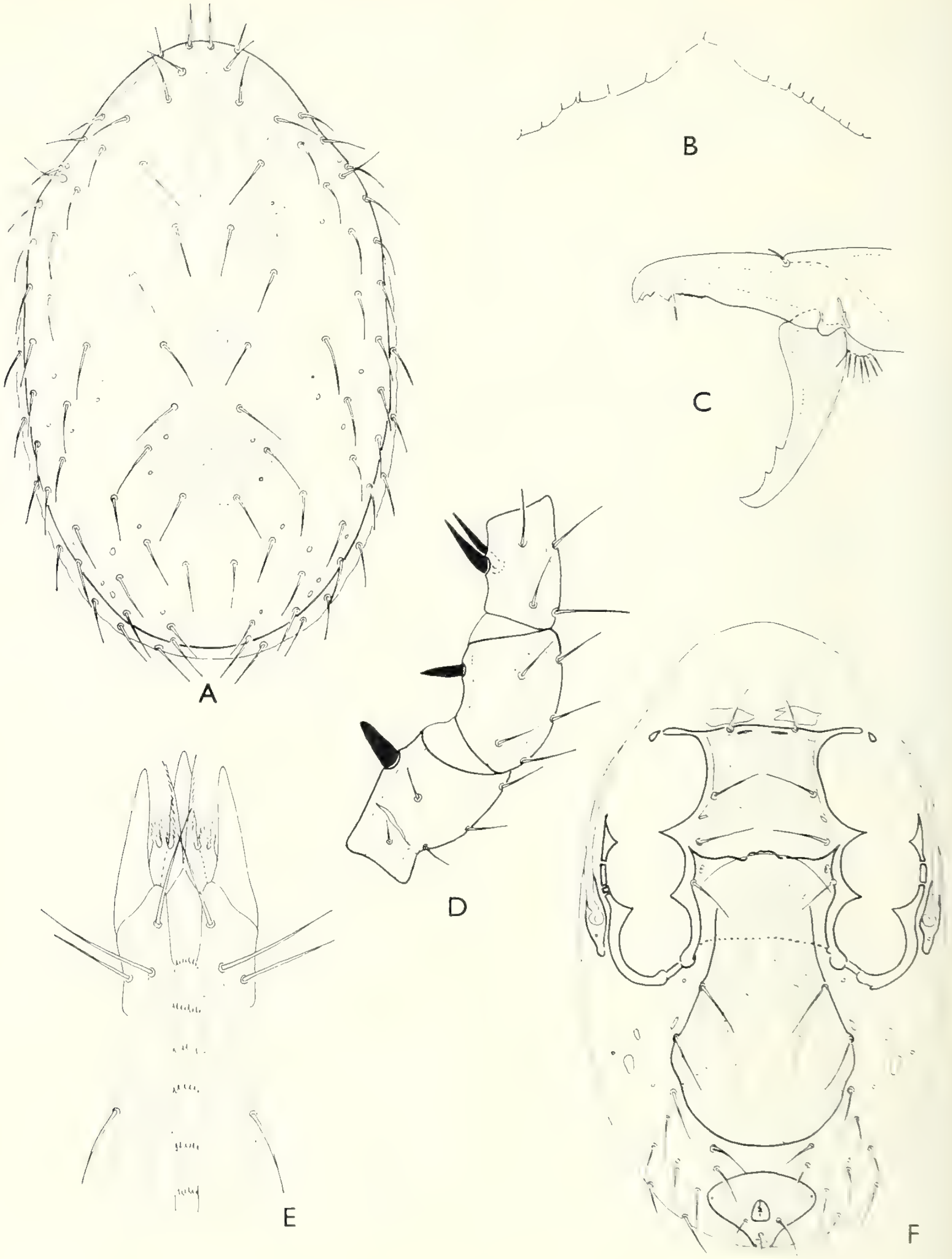


FIG. 20. *Hypoaspis sardoa* (Berlese), female ; dorsum of idiosoma (A) ; tectum (B) ; chelicera (C) ; femur, genu and tibia of leg II (D) ; deutosternum and hypostome (E) ; venter of idiosoma (F).

capituli with denticulate anterior margin (Text-fig. 20B); salivary styli reach nearly to tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (732 μ × 456 μ) with 39 pairs of setae (Text-fig. 20A). Surface of shield reticulated; no hypertrichy; one pair of *r* and six pairs of *R* setae on the cuticle.

Tritosternum with base 48 μ, laciniae 120 μ. Sternal shield (170 μ × 156 μ) with three pairs of setae and two pairs of pores; metasternal setae free with associated pores. Between *st*1, 84 μ; between *st*1 and *st*3, 160 μ. Genital shield (216 μ × 156 μ) flask-shaped, with two pairs of setae. Anal shield (80 μ × 114 μ) with maximum width 140 μ; paranal setae about 66 μ, postanal seta about 33 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 20F. Peritreme extends to anterior margin of coxa II; peritrematal shield has anterior part fused with dorsal shield, posterior part free.

Chaetotaxy of legs differs from normal pattern in that tibia III and genu IV each have a second postero-lateral seta. Femur II has a stout, blunt seta (av_1); genu II has one (av_1) and tibia II has two (av_1 and pv_1) stout, pointed setae (Text-fig. 20D). On tarsus II setae av_{1-2}, pv_{1-2} and *mv* are stout and pointed. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	108/48	114/66	84/48	120/48
tibia	126/45	105/60	90/48	132/48
tarsus	198/42	150/45	170/42	230/40

HABITAT: In litter and in the nests, more rarely on the bodies, of moles and field mice (*Apodemus flavicollis* (Melchior) and *A. sylvaticus* (Linn.)) in Britain, Europe and the U.S.S.R. Recorded by Bregetova from the nest of *Phoenicurus phoenicurus* (Linn.).

Hypoaspis heselhausi Oudemans

Hypoaspis heselhausi Oudemans, 1912, *Ent. Ber. Amst.* **3**: 216.
Bregetova, 1956, *Opred. Faune SSSR.* **61**: 78, figs.

Female: Chelicera with segment I, 45 μ; II, 126 μ; movable digit 48 μ, bidentate; fixed digit with five teeth, pilus dentilis short, setiform, dorsal seta a little longer and stouter than the pilus (Text-fig. 21C). Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp.*2 about 30 μ apart. Deutosternum with six transverse rows of denticles (4–6 per row); corniculi 36 μ long; internal malae as in Text-fig. 21B. Tectum capituli with anterior margin smooth. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (480 μ × 280 μ) with 39 pairs of short, simple setae distributed as in Text-fig. 21A. Surface of shield with scale-like markings.

Tritosternum with base 36 μ, laciniae 72 μ. Sternal shield (108 μ × 102 μ) with three pairs of setae and two pairs of pores; metasternal setae free with associa-

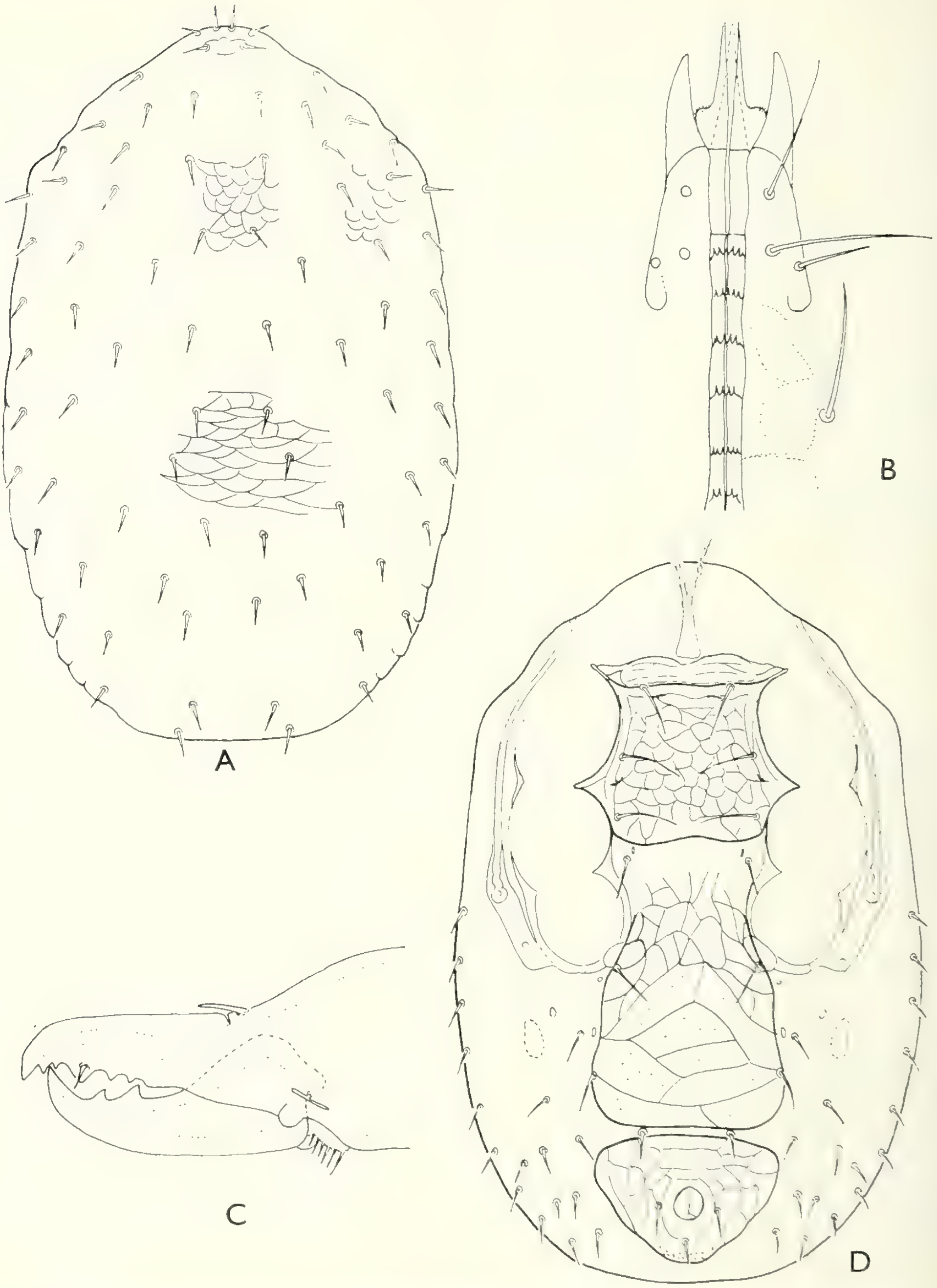


FIG. 21. *Hypoaspis heselhausi* Oudemans, female ; dorsum of idiosoma (A) ; deutosternum and hypostome (B) ; chelicera (C) ; venter of idiosoma (D).

ted pores. Between *st*1, 56 μ; between *st*1 and *st*3, 96 μ. Genito-ventral shield (108 μ × 84 μ) with maximum width (135 μ) near posterior margin, bearing a pair of genital and a pair of opisthogastric setae. Anal shield (75 μ × 105 μ) with maximum width (117 μ) near anterior margin; paranal setae 20 μ, postanal seta 18 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 21D. Peritreme extends to middle of coxa I; anterior tip of peritrematal shield fused with dorsal shield, posterior part completely or incompletely fused with podal shield of coxa IV.

Legs with normal chaetotaxy. Cuticle of legs with warty appearance. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	60/27	57/38	36/30	57/33
tibia	63/27	48/36	36/30	57/30
tarsus	108/25	72/27	80/24	90/27

HABITAT: In the nests of *Talpa europaea* Linn. and *Microtus arvalis* (Pallas) in Britain, the Netherlands and the U.S.S.R. We have also examined specimens from the nest of *Bombus lapidarius* (Linn.) at Langley Park, Buckinghamshire (coll. K. F. Colombo).

Hypoaspis nidicorva sp. nov.

Female: Chelicera with segment I, 70 μ; II, 180 μ; movable digit 75 μ, bidentate; fixed digit tridentate; pilus dentilis short, setiform (Text-fig. 23E) Four pairs of gnathosomal setae with *c.s.* about 54 μ apart, *hyp.*2 about 42 μ apart. Deutosternum with six transverse rows of denticles (6–7 per row); corniculi 66 μ long; internal malae with a deep fringe as in Text-fig. 23F. Tectum capituli with anterior margin smooth (Text-fig. 23B). Salivary styli conspicuous, extending a little beyond tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (624 μ × 384 μ) with 39 pairs of setae and three accessory setae distributed as in Text-fig. 22A. Surface of shield reticulate and granular.

Tritosternum with base 48 μ, laciniae 102 μ. Sternal shield (110 μ × 130 μ) granular, anterior two-thirds reticulate, with three pairs of setae and two pairs of pores. Metasternal setae free with associated pores. Between *st*1, 70 μ; between *st*1 and *st*3, 105 μ. Genito-ventral shield (216 μ × 120 μ) flask-shaped, posterior margin truncate, very close to anal shield; bearing one pair of genital and three pairs of opisthogastric setae. Between *Jv*2, 162 μ. Anal shield (78 μ × 105 μ) with maximum width at anterior margin (132 μ); paranal setae 30 μ; postanal seta 45 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 22B. Peritreme extends beyond posterior margin of coxa I; anterior part of peritrematal shield fused with dorsal shield; posterior part fused with podal shield of coxa IV.

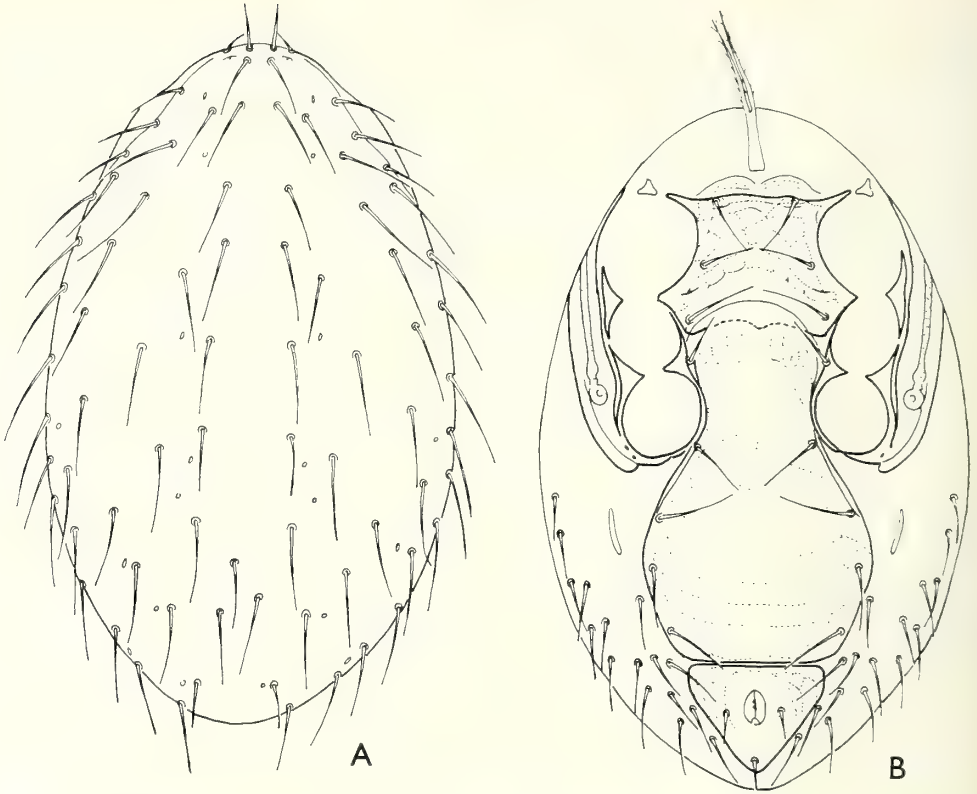


FIG. 22. *Hypoaspis nidicorva* sp. nov., female ; dorsum (A) and venter (B) of idiosoma.

Chaetotaxy of legs normal. Dorsal seta on trochanter IV relatively stout. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	84/36	75/42	54/30	78/30
tibia	90/30	70/42	54/30	80/27
tarsus	132/30	102/30	110/24	162/24

Male : Chelicera with segment I, 40 μ ; II, 117 μ ; movable digit 45 μ, as long as spermadactyl, unidentate ; fixed digit unidentate, pilus dentilis short, setiform (Text-fig. 23C). Four pairs of gnathosomal setae with *c.s.* about 40 μ apart, *hyp.2* about 36 μ apart. Corniculi 48 μ long. Deutosternum, internal malae, tectum and pedipalps as in female.

Dorsal shield (396 μ × 267 μ) as in female, with 39 pairs of setae and one or two accessory setae. Tritosternum with base 36 μ, laciniae 105 μ. Holoventral shield (360 μ × 96 μ) with four pairs of setae and three pairs of pores in the sternal region, one pair of genital and five pairs of opisthogastric setae in the genito-ventral region (Text-fig. 23A). Between *st*1, 48 μ; between *st*1 and *st*3, 90 μ. Paranal setae 24 μ; postanal seta 36 μ. Peritreme extends beyond posterior margin of coxa I; anterior part of peritrematal shield fused with dorsal shield, posterior part fused with holoventral shield and with podal shield of coxa IV.

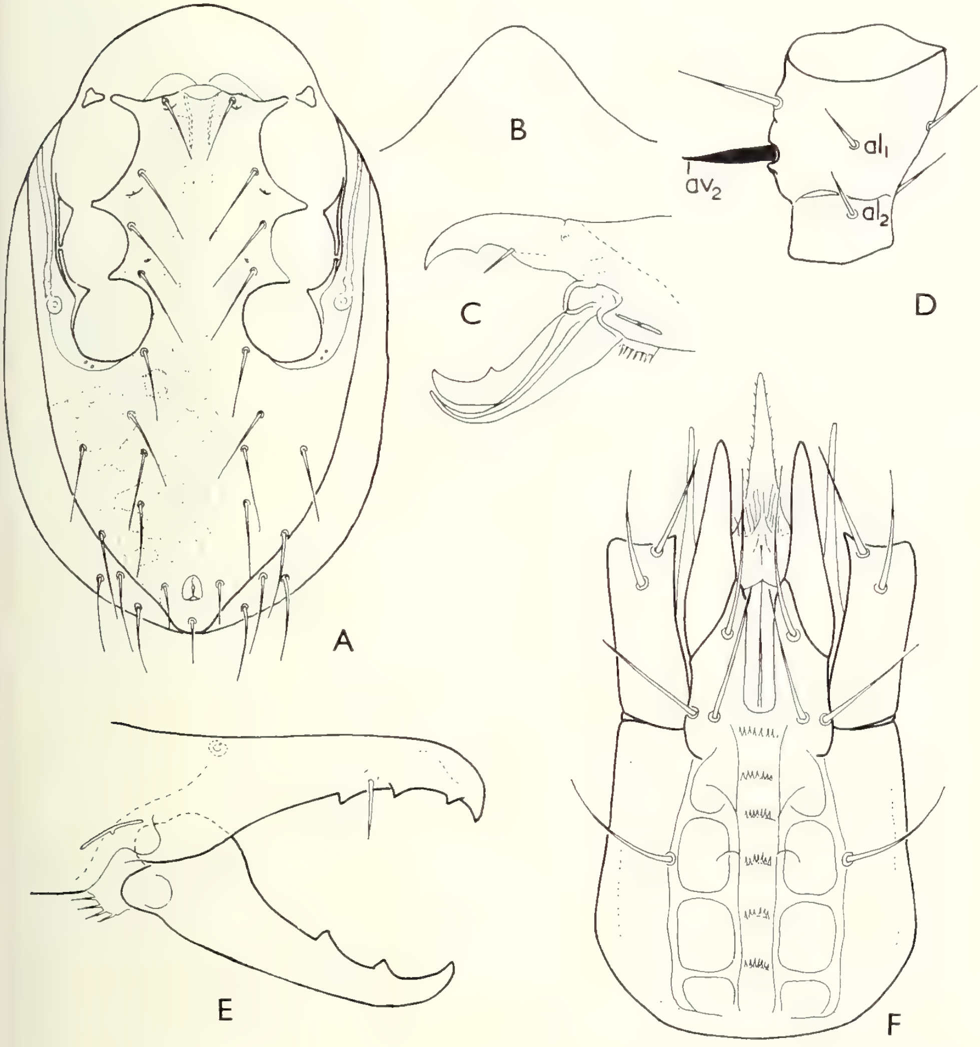


FIG. 23. *Hypoaspis nidicorva* sp. nov. A. Venter of idiosoma of male; B. tectum capituli of female; C. chelicera of male; D. femur II of male; E. chelicera of female; F. venter of gnathosoma of female.

Chaetotaxy of legs as in female. Femur II with seta av_2 very stout and spine-like (Text-fig. 23D). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	63/27	60/36	40/22	60/20
tibia	70/24	50/33	40/24	63/22
tarsus	105/24	75/26	84/21	126/21

Deutonymph : Chelicera with segment I, 50 μ ; II, 156 μ ; movable digit 60 μ. Gnathosoma generally as in female ; setae *c.s.* about 48 μ apart, *hyp.*2 about 36 μ apart ; corniculi 45 μ long.

Dorsal shield (444 μ × 246 μ) with lateral incisions ; with 14 pairs of setae in the podonotal region, the *s* series and the humeral seta being on the striated cuticle ; opisthonotal region with the usual 17 pairs of setae and two accessory setae. Tritosternum with base 45 μ, laciniae 84 μ. Sternito-genital shield (246 μ × 114 μ) with four pairs of setae and three pairs of pores ; between *st*1, 70 μ ; between *st*1 and *st*3, 108 μ. Anal shield (66 μ × 75 μ) triangular with maximum width (100 μ) at anterior margin ; paranal setae 24 μ, postanal seta 40 μ. Peritreme extends beyond posterior margin of coxa I ; peritrematal shield free anteriorly, posterior part not developed.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	70/30	63/42	45/27	63/27
tibia	72/30	54/40	45/30	63/27
tarsus	108/27	84/27	90/24	132/24

HABITAT : Nest of a Jackdaw, Wookey Hole, Somerset, Britain, collected by O. C. Lloyd, 11th September, 1957. Holotype female (1965 : 12 : 29 : 27), allotype male (1965 : 12 : 29 : 28).

Hypoaspis claviger (Berlese)

Laelaps claviger Berlese, 1883, *Acari, Myr. Scorp. Ital.* fasc. 4, no. 2.

Female : Chelicera with segment I, 60 μ ; II, 156 μ ; movable digit 60 μ, bidentate ; fixed digit with four teeth (Text-fig. 24G) ; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 57 μ apart, *hyp.*2 about 42 μ apart. Deutosternum with six transverse rows of denticles (2–6 per row) ; corniculi 50 μ long ; internal malae branched (Evans & Till, 1965 ; Text-fig. 4A). Tectum capituli with denticulate anterior margin. Salivary stylus reaches tip of corniculus. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (654 μ × 366 μ) with the normal 39 pairs of setae and four unpaired accessory setae, all spatulate in shape (Text-fig. 24C) and arranged as in Text-fig. 24A. Surface of shield reticulate ; seven pairs of *R* setae on the cuticle.

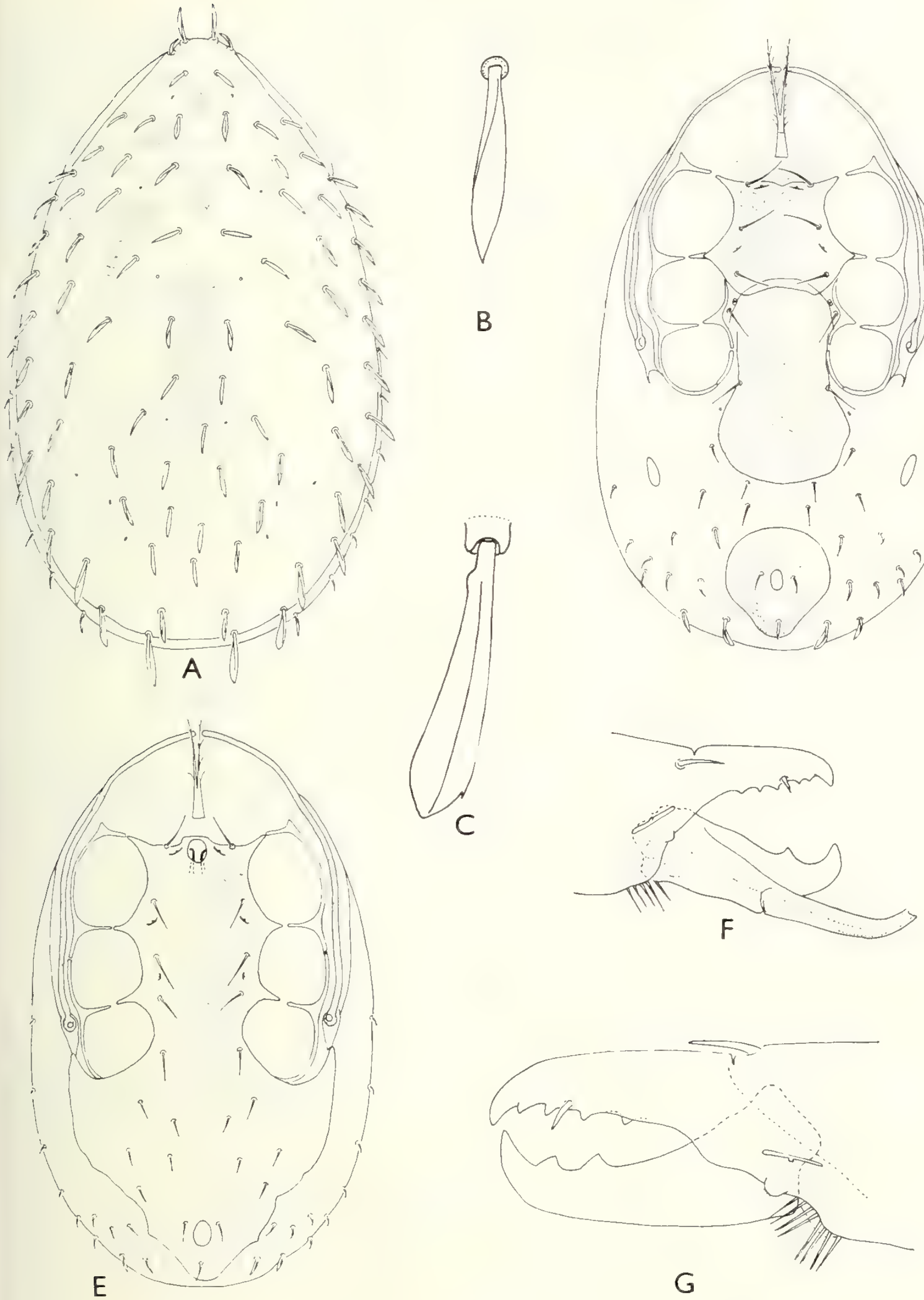


FIG. 24. *Hypoaspis claviger* (Berlese). A. Dorsum of idiosoma of female; B. dorsal seta *J*4 of female; C. dorsal seta *Z*5 of female; D. venter of idiosoma of female; E. venter of idiosoma of male; F. chelicera of male; G. chelicera of female.

Tritosternum with base 45 μ, laciniae 80 μ. Sternal shield (110 μ × 110 μ) with three pairs of setae and two pairs of pores; metasternals free with associated pores. Between *st*1, about 70 μ; between *st*1 and *st*3, 102 μ. Genital shield flask-shaped (105 μ × 102 μ), with one pair of setae. Anal shield (102 μ × 114 μ) with paranal and postanal setae about 20 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 24D. Peritremes reach midpoint at anterior end of idiosoma; peritrematal shields free anteriorly, posterior part fused with podal elements of coxa IV.

Legs with normal chaetotaxy. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	100/40	80/50	63/45	87/45
tibia	100/33	70/48	60/45	90/48
tarsus	153/27	138/40	140/36	216/36

Male: Chelicera with segment I, 42 μ; II, 108 μ; movable digit 40 μ, unidentate; spermadactyl as in Text-fig. 24F; fixed digit bidentate. Four pairs of gnathosomal setae with *c.s.* about 48 μ apart, *hyp.* 2 about 36 μ apart. Deutosternum with six transverse rows of denticles (2–5 per row); corniculi 36 μ long. Other gnathosomal features as in female.

Dorsal shield (486 μ × 282 μ) with 39 pairs of setae and five unpaired accessory setae; seven pairs of *R* setae on the cuticle. Tritosternum with base 30 μ, laciniae 60 μ. Holoventral shield (360 μ × 96 μ) with three pairs of sternal, one pair of metasternal setae and three pairs of pores in the sternal region; between *st*1, 54 μ; between *st*1 and *st*3, 93 μ. Genito-ventral region with six pairs of setae; paranal setae 18 μ, postanal seta 15 μ. Chaetotaxy of opisthogaster, including *R* series, as in Text-fig. 24E. Peritremes reach mid-anterior point of idiosoma; peritrematal shields fused anteriorly with dorsal shield, posteriorly with holoventral shield.

Legs with normal chaetotaxy. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	80/36	63/42	50/36	78/40
tibia	80/30	56/40	48/36	80/36
tarsus	135/24	117/30	120/30	170/33

HABITAT: Probably predacious, living in soil, litter and rotting wood. Recorded from Britain and Europe.

Hypoaspis cuneifer (Michael)

Laelaps cuneifer Michael, 1891, *Proc. zool. Soc. Lond.*: 647.
Laelaps (Cosmolaelaps) cuneifer: Berlese, 1904, *Redia* **1**: 416, pl. 15, figs. 123–124, pl. 16, fig. 125.
Cosmolaelaps cuneifer: Bregetova, 1956, *Opred. Faune SSSR.* **61**: 75.

Female: Chelicera with segment I, 78 μ; II, 234 μ; movable digit 84 μ, bidentate; fixed digit with about seven teeth, pilus dentilis short, setiform (Text-fig. 25F).

Four pairs of gnathosomal setae with *c.s.* about 90 μ and *hyp.2* about 72 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 50 μ long ; internal malae with long slender filaments as in Text-fig. 25H. Tectum capituli with denticulate anterior margin (Text-fig. 25D). Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (804 μ × 684 μ) with the normal 39 pairs of setae plus 14 unpaired accessory setae ; all except setae *r1* and *S2* are cuneiform (Text-fig. 25A and C). Surface of shield with reticulations consisting of rows of tiny spine-like markings.

Tritosternum with base 54 μ, laciniae 123 μ. Sternal shield (168 μ × 162 μ) with two pairs of setae and one pair of pores ; first pair of setae and pores situated on granular presternal area. Metasternals free with associated pores. Between *st1*, 72 μ ; between *st1* and *st3*, 153 μ. Genital shield (168 μ × 204 μ) expanded behind genital setae. Anal shield (114 μ × 126 μ) with paranal and postanal setae subequal, 24–30 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 25B. Peritreme extends to middle of coxa I ; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs differs from normal pattern in having two postero-lateral setae on genu IV $(2\text{—}\frac{2}{1}, \frac{3}{0}\text{—}2)$. Most leg setae simple, some dorsal setae (on femora and trochanters) spatulate. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	132/54	108/66	90/54	138/57
tibia	150/45	96/66	90/54	138/54
tarsus	234/42	180/50	186/45	270/42

Male : Chelicera with segment I, 70 μ ; II, 192 μ ; movable digit 66 μ (84 μ with spermadactyl), unidentate ; fixed digit with four distinct teeth and a row of fine serrations. Four pairs of gnathosomal setae with *c.s.* about 75 μ and *hyp.2* about 66 μ apart. Corniculi 45 μ long ; deutosternum, internal malae, tectum and pedipalps as in female.

Dorsal shield (636 μ × 546 μ) with the normal 39 pairs of setae as well as unpaired accessory setae. Surface of shield patterned as in female.

Tritosternum with laciniae approximately three times as long as the base. Holoventral shield (492 μ × 147 μ) with four pairs of setae and three pairs of pores in the sternal region, five pairs of setae in the genito-ventral region (Text-fig. 25E). Between *st1*, 84 μ ; between *st1* and *st3*, 123 μ. Par- and postanal setae subequal in length, about 30 μ. Peritreme extends to middle of coxa I ; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs as in female. In addition, seta av_1 on femur II is large and spine-like (Text-fig. 25G) ; setae *av* on genu and tibia II are considerably stouter than setae *pv*. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	120/48	96/57	78/48	120/54
tibia	120/42	78/54	72/45	120/48
tarsus	198/36	120/42	132/36	198/42

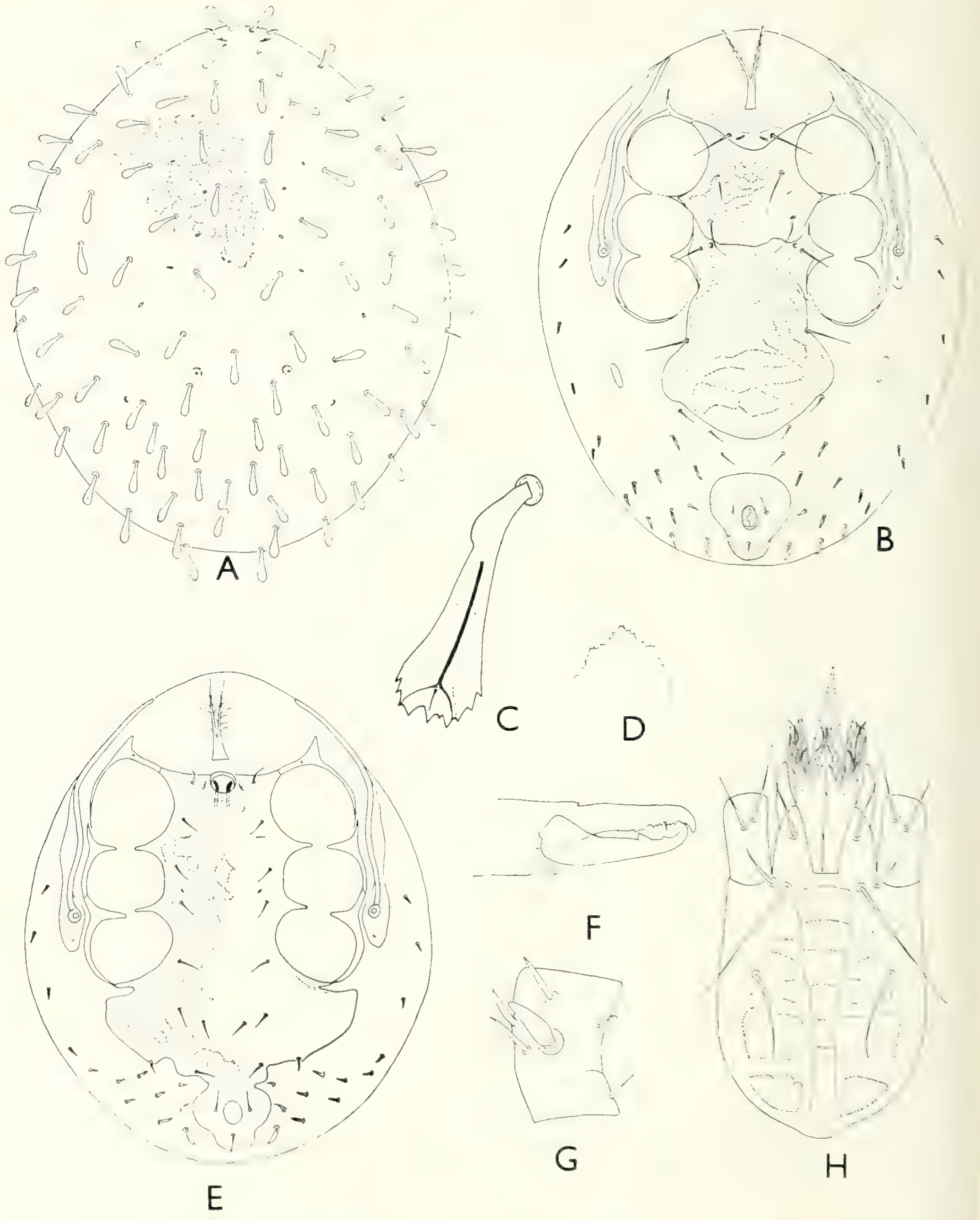


Fig. 25. *Hypoaspis cuneifer* (Michael). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. dorsal seta *z*6 of female; D. tectum capituli of female; E. venter of idiosoma of male; F. chelicera of female; G. femur II of male; H. venter of gnathosoma of female.

HABITAT: Myrmecophilous, associated with many ant hosts. Recorded from Europe, the U.S.S.R. and (?) Britain. We have included this species on the basis of the records given by Hull (1918) and by Turk (1953). It is possible that this species does not occur in Britain, but that its identity has been confused with that of *H. neocuneifer*.

Hypoaspis neocuneifer sp. nov.

Female: Chelicera with segment I, 75 μ; II, 186 μ; movable digit 66 μ, bidentate; fixed digit with from five to nine teeth; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 75 μ apart, *hyp.2* about 57 μ apart. Deutosternum with six transverse rows of small, fine denticles; corniculi 45 μ; internal malae with long, slender filaments as in *H. cuneifer*. Tectum capituli with denticulate anterior margin. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (740 μ × 528 μ) with the normal 39 pairs of setae and about nine unpaired accessory setae distributed as in Text-fig. 26A. Setae cuneiform in shape (Text-fig. 26D). Surface of shield with reticulations consisting of rows of tiny spine-like markings.

Tritosternum with base 45 μ, laciniae 110 μ. Sternal shield (117 μ × 144 μ) with two pairs of setae and one pair of pores, the first pair of setae and pores being situated on the granular pre-sternal area. Metasternal setae free with associated pores. Between *st1*, 80 μ; between *st1* and *st3*, 126 μ. Genital shield (123 μ × 153 μ) flask-shaped, reticulated. Anal shield (110 μ × 108 μ) with paranal setae simple, 27 μ long; postanal seta spatulate, 24 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 26B. Peritreme extends to about anterior third of coxa I; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Legs with normal chaetotaxy. Most leg setae simple, but rather short and spine-like, except at tip of tarsus I; some dorsal setae (on trochanters I, III, IV, and femora II–IV) spatulate. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	120/48	102/60	84/50	120/54
tibia	132/42	84/54	78/48	120/48
tarsus	186/36	144/45	156/42	225/42

Male: Chelicera with segment I, 50 μ; II, 165 μ; movable digit 58 μ, unidentate; spermadactyl 84 μ long from base of movable digit; fixed digit with about nine small teeth, pilus dentilis short, setiform (Text-fig. 26E). Four pairs of gnathosomal setae with *c.s.* about 63 μ apart, *hyp.2* about 50 μ apart. Corniculi 36 μ long; deutosternum, internal malae, tectum and pedipalps as in female.

Dorsal shield (624 μ × 408 μ) with 39 pairs of setae and about nine unpaired accessory setae. Surface of shield as in female.

Tritosternum with base 33 μ, laciniae 90 μ. Venter bears a sternito-genito-ventral shield (336 μ × 126 μ) and a separate anal shield (110 μ × 96 μ); the former

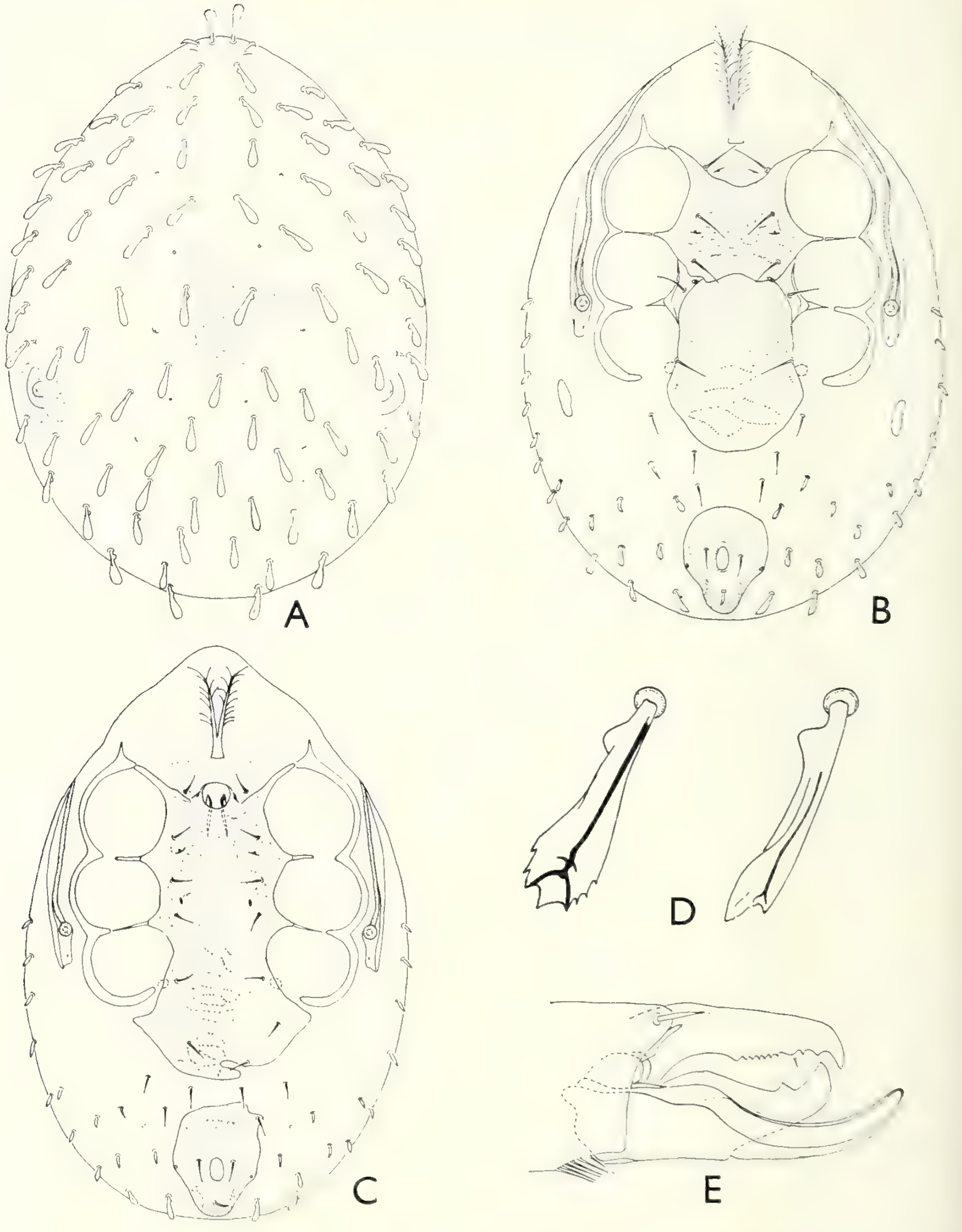


FIG. 26. *Hypoaspis neocuneifer* sp. nov. A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. venter of idiosoma of male ; D. setae z4 and z6 of female ; E. chelicera of male.

with four pairs of sternal setae and three pairs of pores, a pair of genital setae and three to five opisthogastric setae (Text-fig. 26c). Between *st*1, 70 μ; between *st*1 and *st*3, 102 μ. Paranal setae 24 μ, postanal seta 18 μ long.

Chaetotaxy of legs and form of setae as in female; in addition, seta av_1 on femur II stout and spine-like. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	99/42	84/54	66/45	102/48
tibia	105/38	78/50	66/42	102/45
tarsus	150/33	114/42	126/40	186/38

HABITAT: Nests of *Formica rufa* Linn., White Hill Wood, Canterbury, 1st November, 1942 and 25th April, 1942. Holotype ♀ (1965 : 12 : 29 : 23), allotype ♂ (1965 : 12 : 29 : 24), four female paratypes. Ants' nest, White Hill, Canterbury, 18th October, 1941, one male, four female paratypes. Chip nest, same locality, 29th March, 1943, one female paratype. All specimens collected by Dr. E. Warren and deposited in the collection of the British Museum (Natural History).

It is possible that this species has been confused with *Hypoaspis cuneifer* (Michael). The specimens of *H. cuneifer* in the Donisthorpe collection are referable to the new species. We have not seen material of the true *H. cuneifer* in Britain.

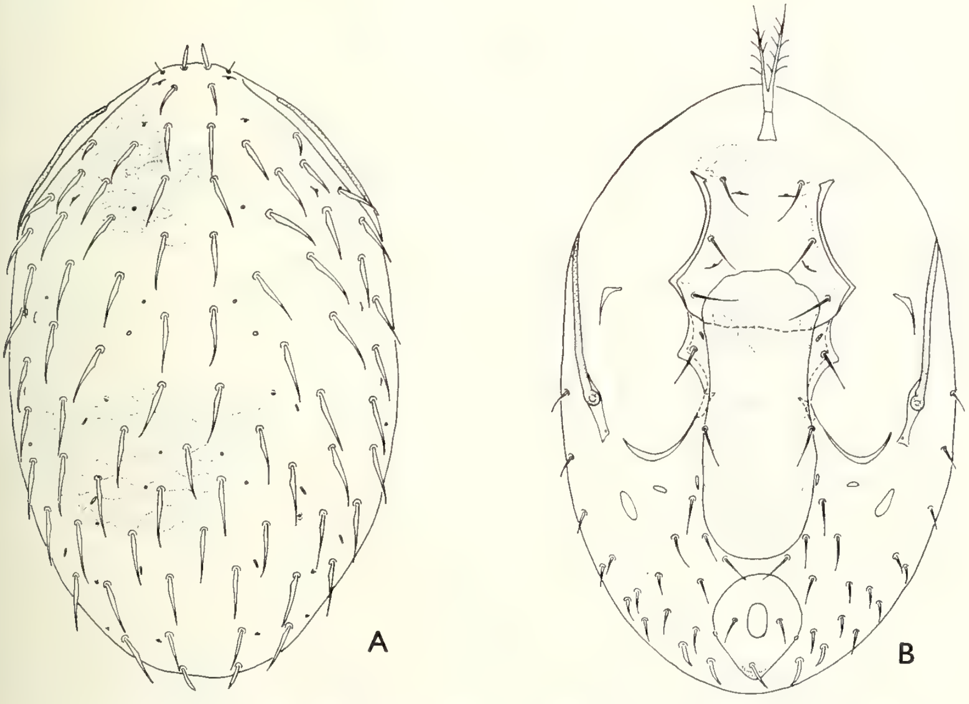


FIG. 27. *Hypoaspis vacua* (Michael), female; dorsum (A) and venter (B) of idiosoma.

Hypoaspis vacua (Michael)

Laelaps vacua Michael, 1891, *Proc. zool. Soc. Lond.*: 651, figs.
Laelaps (*Cosmolaelaps*) *vacuus:* Berlese, 1904, *Redia* **1** : 419, figs.
Laelaps (*Cosmolaelaps*) *vacuus* var. *ensiger* Berlese, 1904, *Redia* **1** : 420, figs.

Female : Chelicera with segment I, 33 μ ; II, 96 μ ; movable digit 33 μ, bidentate ; fixed digit with five teeth, pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with 6 or 7 transverse rows of denticles ; corniculi 27 μ long ; internal malae difficult to discern, but appear to consist of at least two pairs of delicate filaments. Tectum capituli with denticulate anterior margin. Salivary styli slender, reaching to tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (420 $\mu \times$ 264 μ) with the normal 39 pairs of setae and two unpaired accessory setae distributed as in Text-fig. 27A. All the setae except *z*1 are scimitar-like. Surface of shield reticulate.

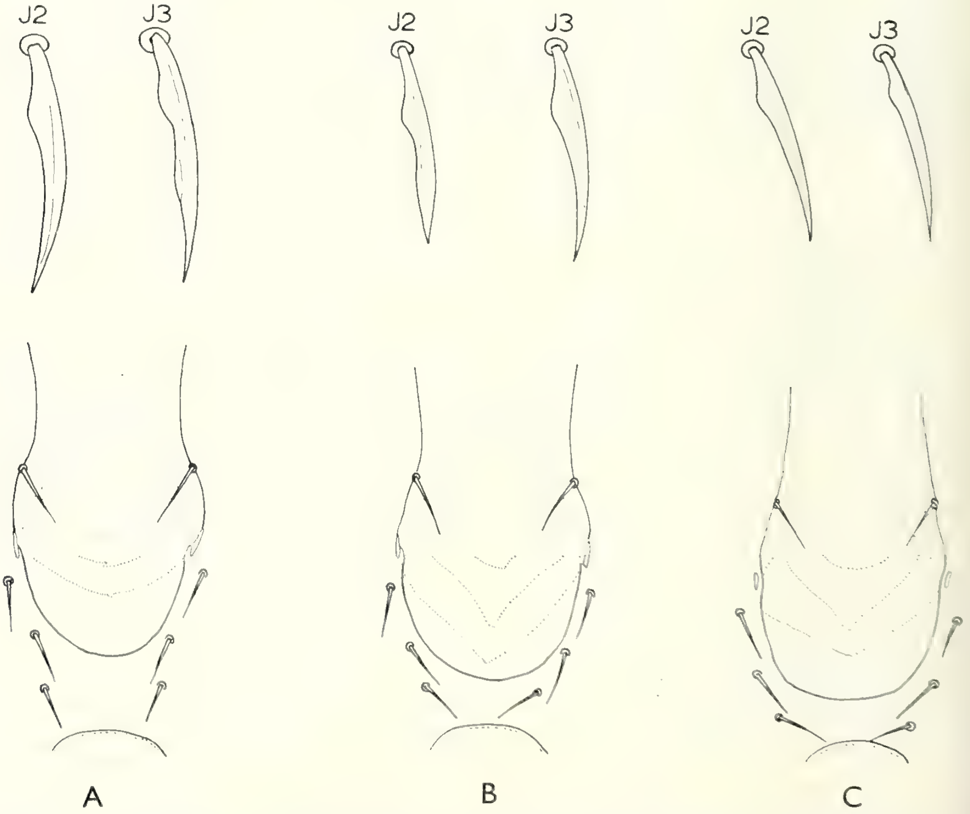


FIG. 28. *Hypoaspis vacua* (Michael), female. Variation in the form of dorsal setae *J*2 and *J*3 and of the genital shield in (A), the type specimen from Igls (Austria) ; in (B), a specimen from Eire, and in (C), a specimen from Sussex (England).

Tritosternum with base 30 μ, laciniae 72 μ. Sternal shield (93 μ × 90 μ) with anterior margin extremely indistinct, bearing three pairs of setae and two pairs of pores; metasternals free with associated pores. Between *st*1, 54 μ; between *st*1 and *st*3, 70 μ. Genital shield (90 μ × 78 μ) with lateral margins almost parallel; bearing genital setae only. Anal shield (66 μ × 63 μ) with paranal setae 18 μ long, postanal seta 21 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 27B. Peritremes extend to middle of coxa I; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

In the limited material of this species which we have examined there appears to be considerable intraspecific variation in the length of the dorsal setae and in the form of the genital shield (Text-figs. 28A–C).

Legs with normal chaetotaxy. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	60/30	51/33	36/27	60/33
tibia	66/24	45/33	33/27	63/30
tarsus	117/24	84/27	72/24	111/27

HABITAT: Moss on tree stumps, Beckley, Sussex, 19th May, 1951; on Isle of Rhum, Scotland, July, 1964; ants' nest, Leigh-on-Sea, Essex, 14th May 1951; Mulranny, Eire, September, 1913; ants' nests in Austria and Italy.

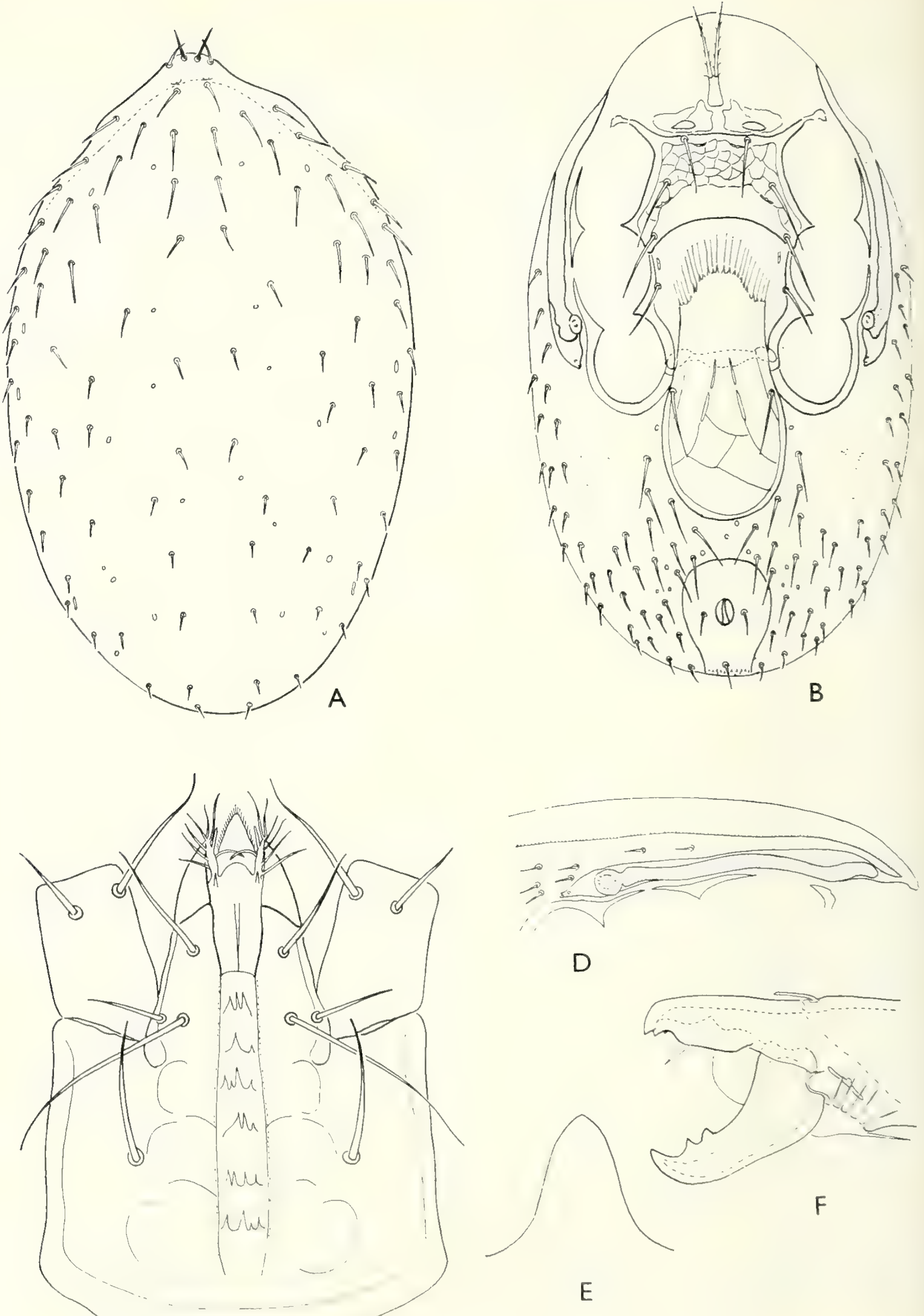
Hypoaspis bombicolens (Canestrini)

Iphis bombicolens Canestrini, 1884, *Prosp. Acarof. Ital.* (6) **2**: 1634.

Female: Chelicera with segment I, 42 μ; II, 108 μ; movable digit 38 μ, bidentate; fixed digit with one large and one small tooth, pilus dentilis short, setiform; dorsal seta short, slender (Text-fig. 29F). Four pairs of gnathosomal setae with *c.s.* about 54 μ apart, *hyp*.2 about 38 μ apart. Deutosternum with six transverse rows of denticles (2–4 per row); corniculi 27 μ; internal malae as in Text-fig. 29C. Tectum capituli with smooth anterior margin (Text-fig. 29E). Salivary styli slender, nearly reaching tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (672 μ × 384 μ) with at least 40 pairs of setae, *px*1 being present on the opisthonotal part (in the specimen figured seta *px*3 is missing on one side). In addition, a variable number of marginal setae are included on both the podonotal and opisthonotal regions of the shield (Text-fig. 29A). Several anterior setae of the *j*, *z*, *s* and *r* series are considerably longer than the remaining setae. Surface of shield granular and reticulate; no hypertrichy.

Tritosternum with base 24 μ, laciniae 81 μ. Sternal shield (84 μ × 138 μ) with three pairs of setae and two pairs of pores, metasternal setae free with associated pores. Between *st*1, 87 μ; between *st*1 and *st*3, 99 μ. Genital shield (120 μ × 105 μ) with genital setae only. Anal shield (96 μ × 70 μ) with paranal setae 18 μ, postanal seta 21 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 29B.


A
B
C
D
E
F

Peritreme extends to anterior third of coxa I ; peritrematal shield fused anteriorly with dorsal shield (Text-fig. 29D) ; posterior part free.

Chaetotaxy of legs differs from normal pattern in that genu IV has two ventral setae ($2—\frac{2}{1}, \frac{3}{1}—1$). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	75/45	75/57	50/48	72/45
tibia	50/40	66/50	54/42	75/40
tarsus	132/36	102/40	120/36	144/33

HABITAT : Recorded from *Bombus terrestris* (Linn.) in Essex, Britain, and from *Bombus* sp. in Italy.

Hypoaspis breviseta sp. nov.

Female : Chelicera with segment I about 50 μ ; II, 120 μ. Structural details are not visible as the chelicerae are retracted. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 45 μ apart. Deutosternum with six transverse rows of denticles (1–6 per row) ; corniculi 30 μ ; internal malae similar to those of *H. bombicolens*, but with the addition of a pair of slender, inner processes. Tectum capituli with smooth anterior margin. Salivary styli nearly reaching tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (744 μ × 456 μ) with 42–44 pairs of setae distributed as in Text-fig. 30A. Setae *px*1–3 are present in the opisthonotal region ; additional marginal setae are present both in the podonotal and the opisthonotal region, but there are no accessories between the *J* series. The setae are short and simple, *j*1 being relatively stout and *Z*5 having the form indicated in Text-fig. 30B. Surface of shield granular.

Tritosternum with base 27 μ, laciniae 84 μ. Sternal shield (84 μ × 150 μ) granular, reticulations very faint except in the antero-lateral corners ; with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 75 μ ; between *st*1 and *st*3, 102 μ. Genital shield (144 μ × 150 μ) granular, with genital setae only. Anal shield (123 μ × 108 μ) granular ; paranal setae 30 μ long, postanal seta broken. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 30C. Peritreme extends to middle of coxa I ; peritrematal shield fused anteriorly with dorsal shield ; posterior part free.

Chaetotaxy of legs differs from free-living pattern in that genu IV bears two ventral setae (*pv* present). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	78/48	75/66	66/54	90/54
tibia	87/42	72/57	66/48	87/48
tarsus	138/40	120/42	130/40	150/40

FIG. 29. *Hypoaspis bombicolens* (Canestrini), female ; dorsum of idiosoma (A) ; venter of idiosoma (B) ; venter of gnathosoma (C) ; peritreme and peritrematal shield (D) ; tectum capituli (E) ; chelicera (F).

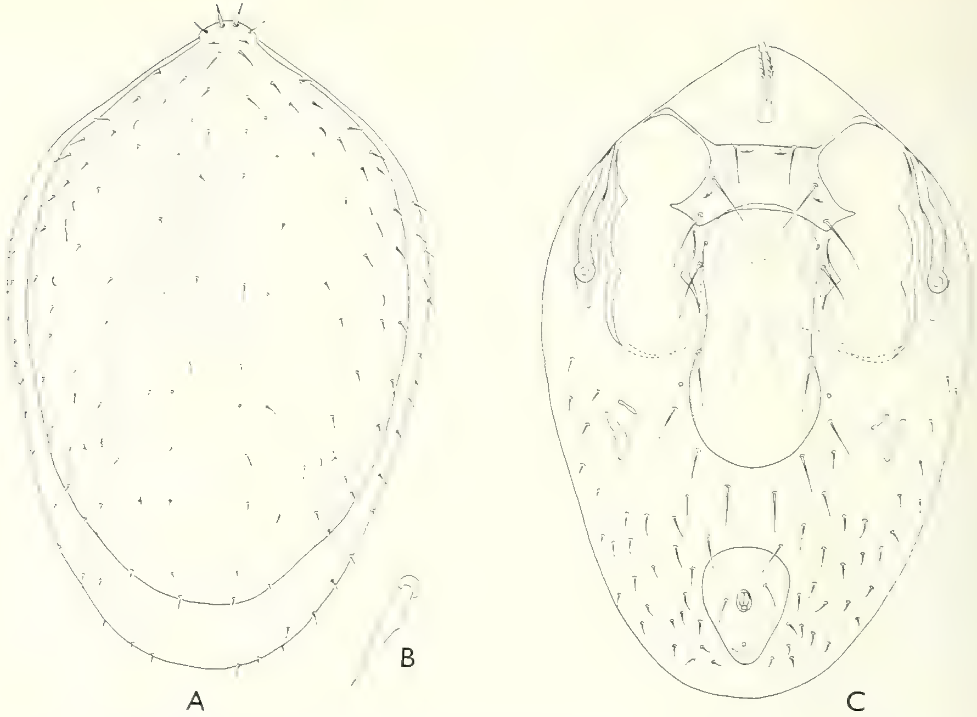


Fig. 30. *Hypoaspis breviseta* sp. nov., female ; dorsum of idiosoma (A) ; seta $Z5$ (B) ; venter of idiosoma (C).

Habitat : On *Bombus muscorum* (Linn.), Scarborough, Yorkshire, October, 1964. Holotype ♀ (1965 : 12 : 29 : 26) in the collection of the British Museum (Natural History).

Hypoaspis colomboi sp. nov.

Female : Chelicera with segment I, 54 μ ; II, 126 μ ; movable digit 45 μ, bidentate ; fixed digit unidentate, pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 40 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 40 μ long ; internal malae with fringed, elongate, inner lobe and fimbriate outer lobe. Tectum capituli with anterior margin smooth, slightly scalloped. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (600 μ × 336 μ) with 38 pairs of setae, *px*2 missing (Text-fig. 31A). Surface of shield granular, no hypertrichy ; marginal cuticle densely setose.

Tritosternum with base about 24 μ, laciniae 80 μ. Presternal area with a pair of pre-endopodal shields. Sternal shield (135 μ × 120 μ) granular, thickened along lateral and anterior margins, with three pairs of setae and two pairs of pores ; metasternal setae and their associated pores situated over the endopodal shields. Between *st*1, 63 μ ; between *st*1 and *st*3, 105 μ. Genital shield (120 μ × 138 μ) with genital setae only. Anal shield (80 μ × 78 μ) with maximum width 86 μ ; paranal setae

36 μ, postanal seta 30 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 31 B. Peritreme extends to about anterior third of coxa I. Peritrematal shield free posteriorly.

Chaetotaxy of legs differs from normal pattern in that genu IV has two ventral setae $\left(2-\frac{2}{1}, \frac{3}{1}-1\right)$. Tarsus II with ventral setae and al_1 and pl_1 stout basally, tapering to fine points. Tarsus IV with ventral setae stout basally, tapering; seta pl_2 stout and spine-like. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	66/33	70/45	42/33	60/33
tibia	80/30	60/42	42/30	63/33
tarsus	130/28	98/33	105/27	135/27

Male: Chelicera with segment I, 45 μ; II, 108 μ; movable digit 36 μ (57 μ with spermadactyl), unidentate; fixed digit unidentate, pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 54 μ apart; *hyp.2* about 42 μ apart; Deutosternum with six transverse rows of denticles; corniculi 36 μ; internal malae triangular. Tectum capituli weakly dentate; pedipalp as in female.

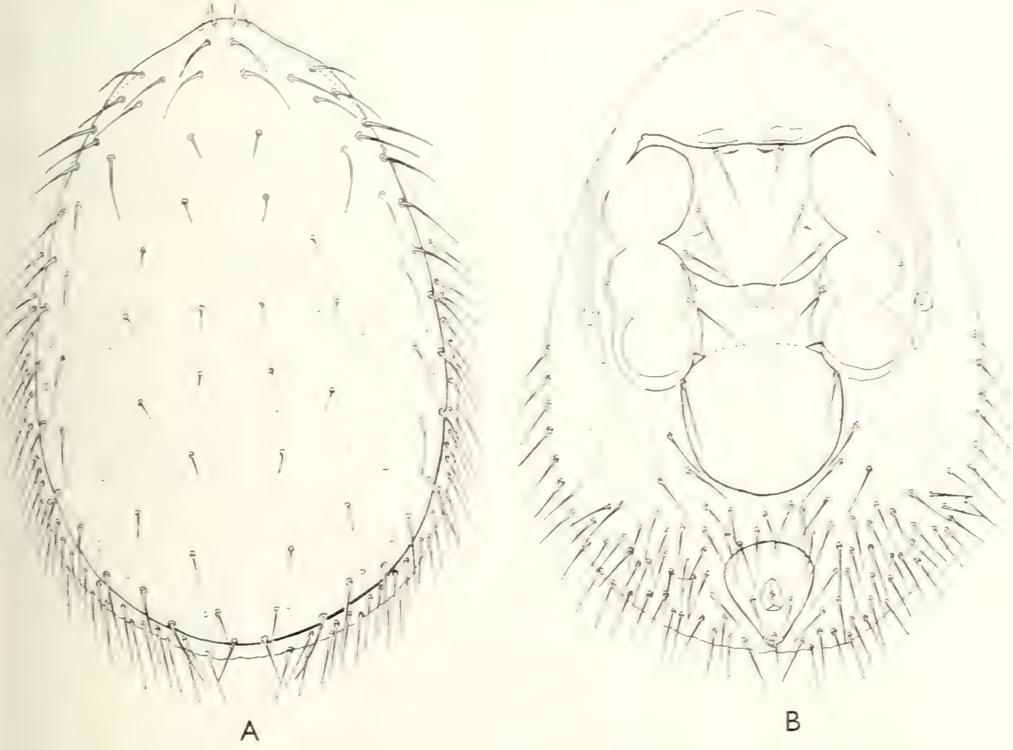


FIG. 31. *Hypoaspis colomboi* sp. nov., female; dorsum (A) and venter (B) of idiosoma.

Dorsal shield (546 μ × 372 μ) as in female. Holoventral shield (420 μ × 102 μ) granular with four pairs of setae and three pairs of pores in the sternal region, one pair of genitals, and about 26 opisthogastric setae (Text-fig. 32D). Between *st*1, 68 μ; between *st*1 and *st*3, 96 μ. Paranal setae 42 μ, postanal seta 33 μ. Peritreme extends to anterior fourth of coxa I; posterior part of peritrematal shield free.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	60/32	63/45	40/27	54/30
tibia	70/27	54/40	42/27	57/27
tarsus	117/27	84/30	84/24	110/24

HABITAT: In nest of *Bombus lapidarius* (Linn.), Langley Park, Buckinghamshire (K.F. Colombo, 1961). Holotype ♀ (1965 : 12 : 29 : 1), allotype ♂ (1965 : 12 : 29 : 2).

Hypoaspis fuscicolens Oudemans

Hypoaspis fuscicolens Oudemans, 1902, *Tijdschr. ned. dierk. Ver.* (2) **7** : 289 (nom. nud.); 1904, *Abh. nat. ver. Bremen* **18** : 83, pl. 4, figs. 23–28.

Female: Chelicerae retracted, details of their structure not clearly visible. Four pairs of gnathosomal setae with *c.s.* very stout and about 72 μ apart, *hyp.*2 about 48 μ apart (Text-fig. 32B). Deutosternum with six transverse rows of denticles (2 to about 8 per row); corniculi 45 μ; internal malae triangular, fringed. Tectum capituli subtriangular with a minute antero-median projection, margin smooth. Pedipalp (2–5–6–14) with three-tined apotele.

Dorsal shield (720 μ × 480 μ) with 24 pairs of setae in the podonotal region, an extra pair of *r* setae being present on the margin and a pair of accessory setae between *j*6. Opisthonotal region of shield hypertrichous (Text-fig. 32A). Surface of shield granular and reticulate.

Tritosternum with base 45 μ, laciniae 105 μ. Sternal shield (84 μ × 186 μ) with three pairs of setae and two pairs of pores, metasternal setae free with associated pores. Between *st*1, 75 μ; between *st*1 and *st*3, 105 μ. Genital shield (130 μ × 150 μ) with genital setae only. Anal shield (132 μ × 108 μ) with par- and postanal setae about 24 μ long. Chaetotaxy and sclerotization of venter as in Text-fig. 32C. Peritreme extends onto dorsum, terminating at a point over posterior margin of coxa I; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs differs from normal pattern in that genu IV has two ventral setae ($2—\frac{2}{1}$, $\frac{3}{1}—1$). Coxae I and II with very stout setae; genu and tibia II with *pv* stouter than *av*; tarus II with seta *mv* short and stout. Ambulacrum I without claws. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	90/50	96/60	66/57	93/57
tibia	96/50	80/63	72/50	99/50
tarsus	140/48	126/50	140/48	168/45

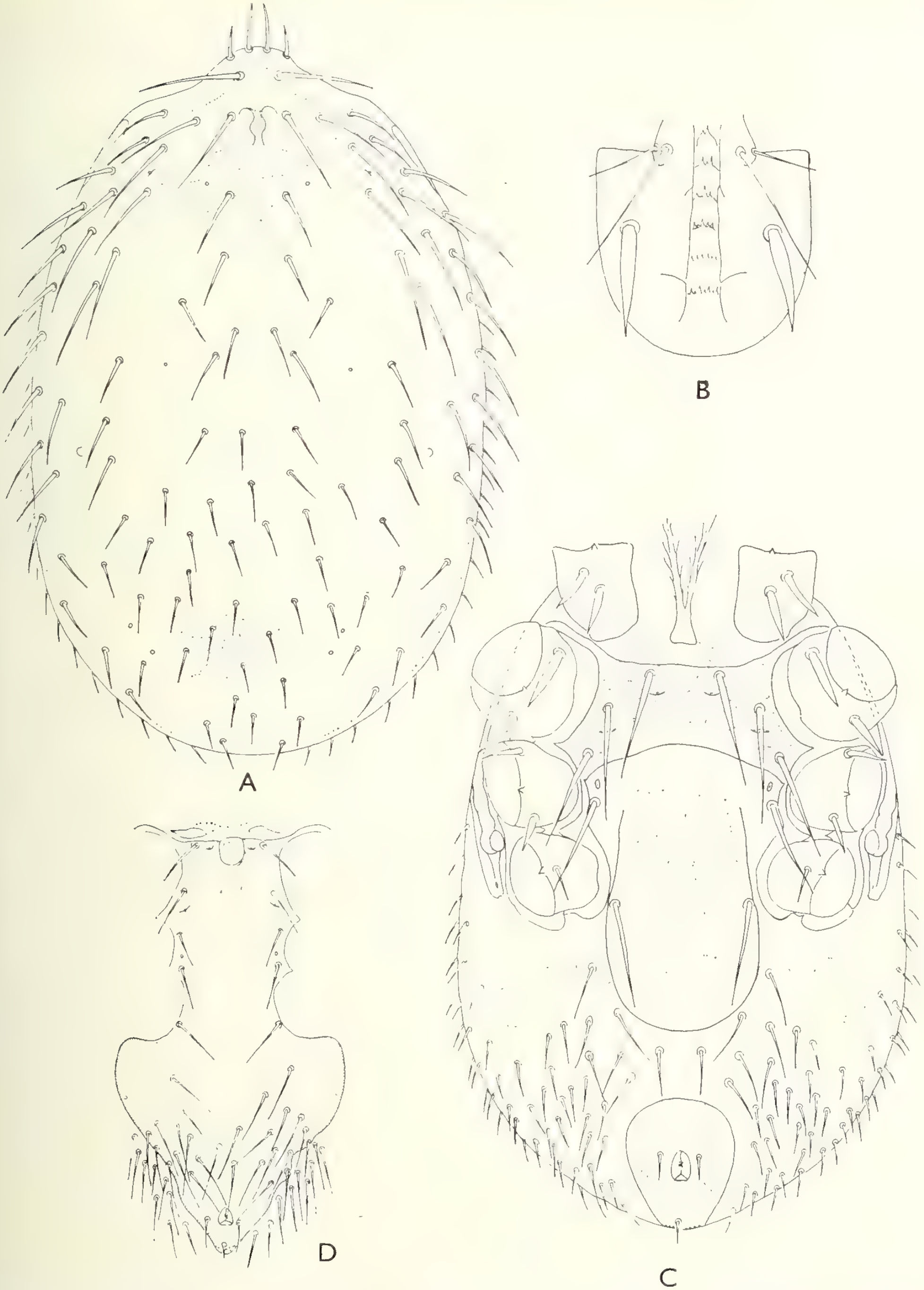


FIG. 32. A–C. *Hypoaspis fuscicolens* Oudemans, female ; dorsum of idiosoma (A) ; basis capituli (B) ; venter of idiosoma (C). D. *Hypoaspis colomboi* sp. nov., male ; holoventral shield.

HABITAT: Found with several species of *Bombus* and with *Psithyrus vestalis* (Geoff.) on Wangeroog Island, Germany.

Hypoaspis hyatti sp. nov.

Female: Chelicera with segment I, 60 μ; II, 120 μ; movable digit 40 μ, bidentate; fixed digit with one large and two minute teeth; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 57 μ apart; *hyp.*2 about 42 μ apart. Deutosternum with six transverse rows of deutosternal teeth (2–6 per row); corniculi 33 μ; internal malae as in *Hypoaspis bombicolens*. Tectum capituli with smooth anterior margin. Salivary styli reach almost to tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (612–642 μ × 396–432 μ) with 43–44 pairs of setae as well as about 16 unpaired accessory setae between the *J* series; *px*1–3 present in opisthonotal region (Text-fig. 33A). Setae simple, slightly longer in the anterior than in the posterior region. Surface of shield granular and reticulate.

Tritosternum with base 30 μ, laciniae 90 μ. Sternal shield (84–90 μ × 132–140 μ) granular and reticulate, with three pairs of setae and two pairs of pores; meta-

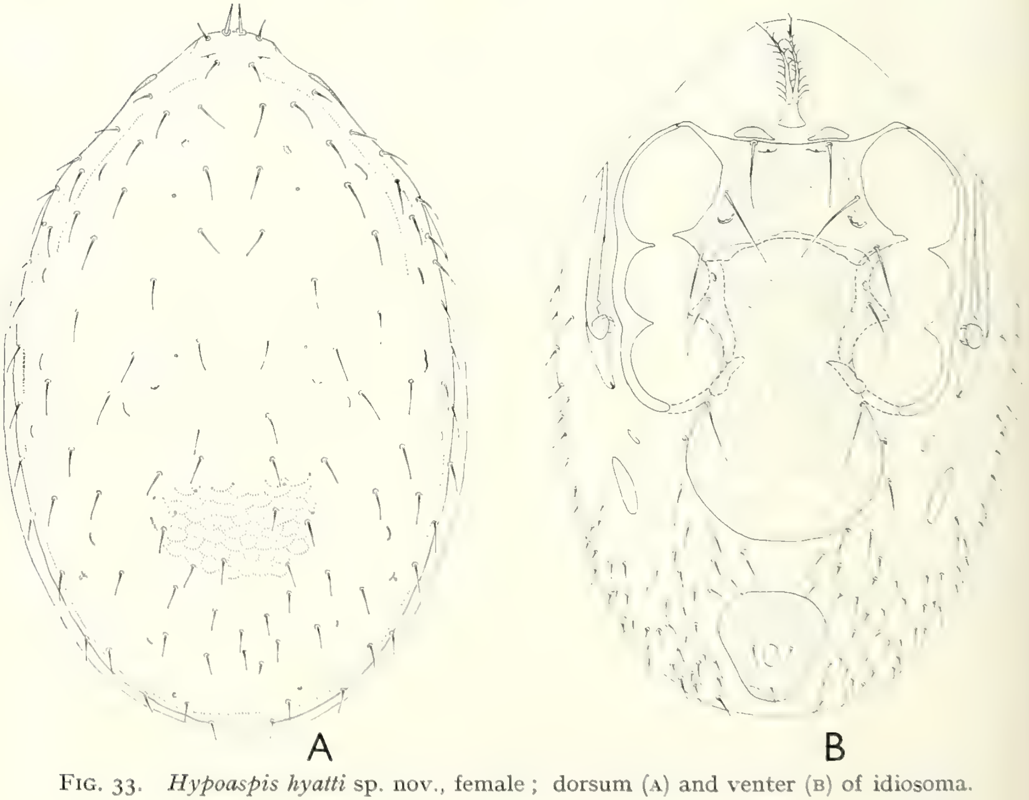


FIG. 33. *Hypoaspis hyatti* sp. nov., female; dorsum (A) and venter (B) of idiosoma.

sternal setae free with associated pores. Between *st*1, 72 μ; between *st*1 and *st*3, 108 μ. A pair of well-defined pre-endopodal shields is situated in the pre-sternal region. Genital shield (130 μ × 150 μ) with genital setae only. Anal shield (93 μ × 84 μ) reticulate; par- and postanal setae about 20 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 33B. Peritreme extends to anterior third of coxa I; anterior part of peritrematal shield fused with dorsal shield; posterior part free.

Chaetotaxy of legs differs from the normal pattern in that genu IV bears two ventral setae (*pv* present). Length/width (in μ) of leg segments:

	I	II	III	IV
genu	84/40	75/54	57/42	75/40
tibia	90/36	68/50	57/36	78/36
tarsus	140/33	110/36	117/33	150/33

HABITAT: On *Bombus muscorum* (Linn.), Scarborough, Yorkshire, October, 1964. Holotype ♀ (1965 : 12 : 29 : 11) and twenty-two female paratypes (1965 : 12 : 29 : 12–22) in the collection of the British Museum (Natural History).

Hypoaspis marginalis (Willmann)

Pneumolaelaps marginalis Willmann, 1953, *Sitz. Österr. Akad. Wiss. Abt.* 1, **162** (6) : 465, figs. 11–12.

Female: Chelicera with segment I, 48 μ; II, 120 μ; movable digit 42 μ, bidentate; fixed digit tridentate, pilus dentilis short, setiform (Text-fig. 34C). Four pairs of gnathosomal setae with *c.s.* about 63 μ apart, *hyp.2* about 48 μ apart. Deutosternum with six transverse rows of denticles (3–8 per row) (Text-fig. 34D); corniculi 30 μ; internal malae with a pair of slender, triangular inner lobes and a pair of fimbriate outer lobes. Tectum capituli with anterior margin smooth. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (624 μ × 408 μ) with 25 pairs of setae in the podonotal region, three pairs of *r* setae apart from the humerals being included on the shield (Text-fig. 34A). Opisthonotal region with 18 pairs of setae, *px*1 being present, and about 13 unpaired accessory setae between the *J* series. Setae near anterior tip of shield noticeably longer than those near posterior tip. Surface of shield granular and reticulate.

Tritosternum with base 33 μ, laciniae about 75 μ. Presternal area with a pair of pre-endopodal shields. Sternal shield (93 μ × 144 μ) with three pairs of setae and two paires of pores. Metasternal setae and associated pores situated over endopodal shields. Between *st*1, 66 μ; between *st*1 and *st*3, 110 μ. Genital shield (110 μ × 147 μ) with genital setae only. Anal shield (90 μ × 90 μ) with paranal setae 21 μ, postanal seta 24 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 34B. Peritreme extends to anterior third of coxa I; posterior part of peritrematal shield free.

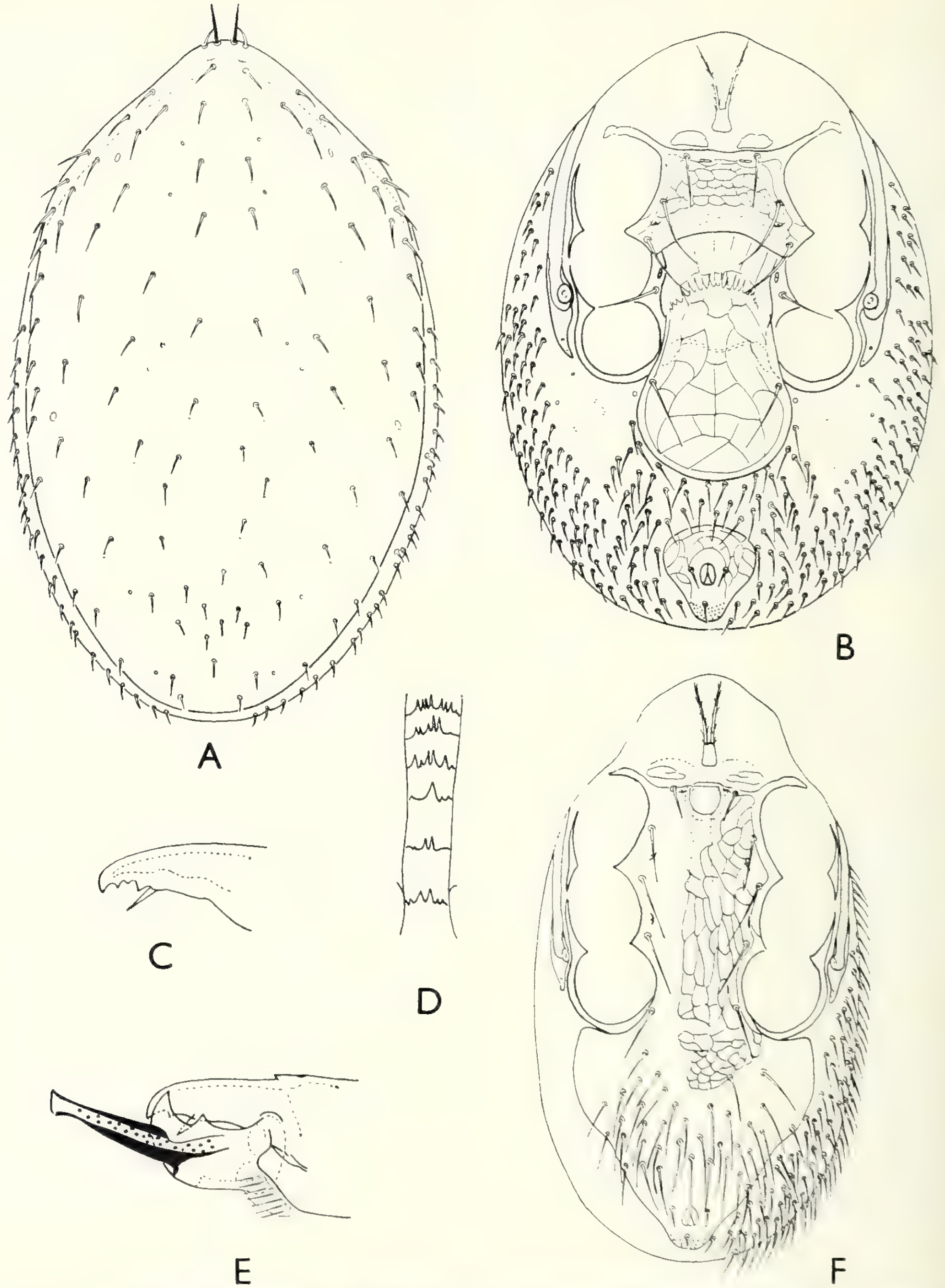


FIG. 34. *Hypoaspis marginalis* (Willmann). A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. fixed digit of chelicera of female ; D. deutosternum of female ; E. chelicera of male ; F. venter of idiosoma of male.

Chaetotaxy of legs differs from the normal pattern in that genu IV has two ventral setae ($2—\frac{2}{1}, \frac{3}{1}—1$). Tarsi II–IV with ventral setae stouter than the dorsals, tarsus IV with setae pl_{2-3} spine-like. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	78/40	75/57	60/44	78/42
tibia	84/36	66/50	57/40	78/38
tarsus	132/33	102/38	117/36	156/33

Male : Chelicera with segment I, 48 μ ; II, 110 μ ; movable digit 36 μ (57 μ with spermadactyl), unidentate ; fixed digit unidentate, pilus dentilis short, setiform (Text-fig. 34E) ; groove of spermadactyl granular. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 42 μ apart. Deutosternum with six transverse rows of denticles (5–6 per row) ; corniculi 36 μ. Internal malae, tectum, capituli and pedipalps as in female.

Dorsal shield (576 μ × 348 μ) with chaetotaxy as in female, but only about six accessory setae. Tritosternum with base 24 μ, laciniae 84 μ. Presternal area with a pair of pre-endopodal shields. Holoventral shield (456 μ × 135 μ) with four pairs of setae and three pairs of pores in the sternal region, with a pair of genital setae and 37–44 opisthogastric setae in the genito-ventral region (Text-fig. 34F). Between *st*1, 66 μ ; between *st*1 and *st*3, 102 μ. Peritreme extends to about middle of coxa I ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs as in female. Femur II with seta av_1 very stout and spine-like ; genu II and tibia II with seta *av* strongly inflated basally ; tarsus II with setae av_{1-2} and *mv* inflated basally, tapering to long fine points. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	78/36	78/60	60/42	78/42
tibia	84/36	66/54	54/36	72/36
tarsus	132/30	96/36	96/30	138/30

HABITAT : Found on *Bombus terrestris* (Linn.) in Essex, in the nest of *B. hortorum* (Linn.) in Hertfordshire, and on *Bombus mucidus* (Gerst.) in Austria.

Hypoaspis minutissima sp. nov.

Female : Chelicera with segment I, 42 μ ; II, 102 μ ; movable digit 36 μ, bidentate ; fixed digit with bifid tip and three small teeth, pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 42 μ ; internal malae slender, indistinct. Tectum capituli with anterior margin smooth. Pedipalp (2–5–6–14) with two-tined apotele.

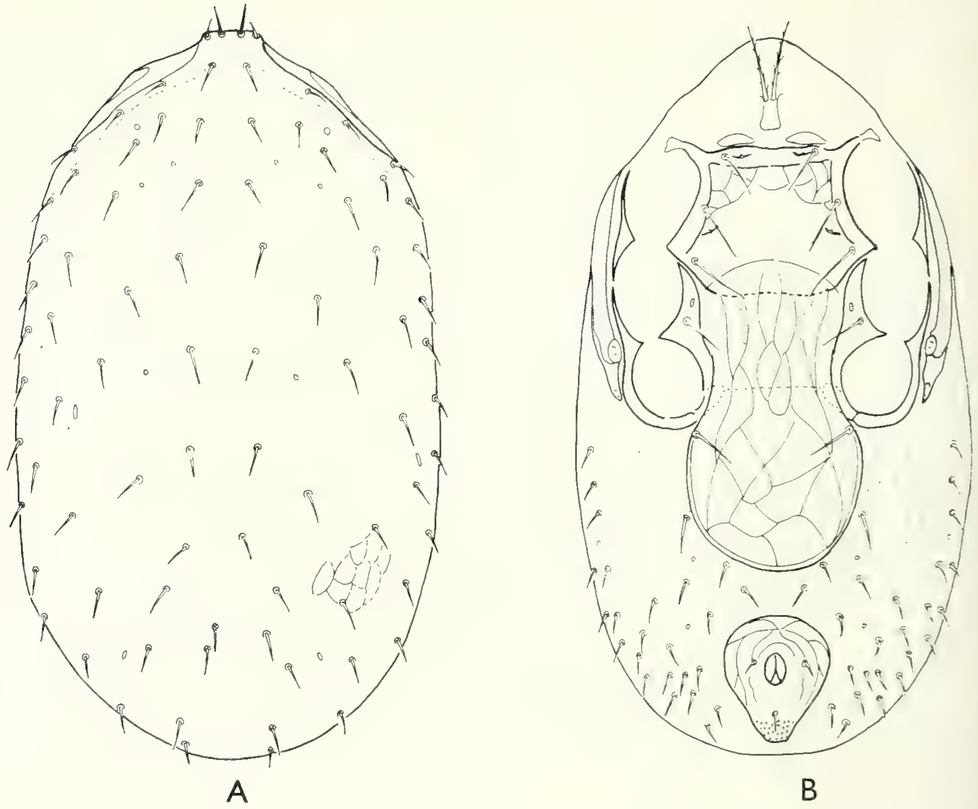


Fig. 35. *Hypoaspis minutissima* sp. nov., female ; dorsum (A) and venter (B) of idiosoma.

Dorsal shield ($492\ \mu \times 312\ \mu$) with 39 pairs of setae and about five accessory setae between the *J* series (Text-fig. 35A). Setae simple, subequal. Surface of shield granular and reticulate.

Tritosternum with base $24\ \mu$, laciniae $84\ \mu$. Presternal area with a pair of pre-endopodal shields. Sternal shield ($105\ \mu \times 105\ \mu$) granular with faint reticulations, bearing three pairs of setae and two pairs of pores. Metasternal setae and associated pores situated over the endopodal shields. Between *st*1, $65\ \mu$; between *st*1 and *st*3, $80\ \mu$. Genital shield ($102\ \mu \times 114\ \mu$) with genital setae only. Anal shield ($60\ \mu \times 75\ \mu$) with paranal setae $15\ \mu$, postanal seta $18\ \mu$. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 35B. Peritreme extends to anterior third of coxa I ; anterior tip of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs differs from normal pattern in that genu IV bears two ventral setae. Tarsi II and IV with ventral setae relatively long, stout basally, tapering to fine points. Seta pl_2 on tarsus IV long, spine-like. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	60/30	60/36	42/27	54/27
tibia	72/27	50/33	42/24	54/24
tarsus	108/27	80/27	96/24	117/24

HABITAT : On a *Bombus terrestris* (Linn.) queen, Gosforth, Cumberland, Britain, collected by D. C. Lee, 3rd May, 1960. Holotype ♀ (1965 : 12 : 29 : 5) and paratype ♀ (1965 : 12 : 29 : 6).

Hypoaspis isotricha (Kolenati)

Holostaspis isotricha Kolenati, 1858, *Wien. Ent. Monatschr.* **2** : 87, figs.

Female : Chelicera with segment II, 66 μ ; movable digit 18 μ, with one minute, subterminal tooth ; fixed digit with one small tooth ; pilus dentilis very short and setiform (Text-fig. 36D). Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 18 μ long ; internal malae as in Text-fig. 36E. Tectum capituli with smooth anterior margin (Text-fig. 36B). Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (612 μ × 432 μ) with 39 pairs of setae and two unpaired accessory setae distributed as in Text-fig. 36A. All the setae except *j*1 and *z*1 are barbed (Text-fig. 36C). Surface of shield sculptured anteriorly, reticulate posteriorly.

Tritosternum with base 36 μ, laciniae about 72 μ. Sternal shield (96 μ × 114 μ) with three pairs of setae and two pairs of pores ; metasternal setae and pores situated over the endopodal shields. Between *st*1, 60 μ ; between *st*1 and *st*3, 108 μ. Genital shield (168 μ × 150 μ) with genital setae only. Anal shield (84 μ × 80 μ) concave anteriorly ; paranal setae 36 μ, postanal seta 60 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 36F. Peritreme extends approximately to anterior margin of coxa II ; posterior part of peritrematal shield free.

Legs with normal chaetotaxy. Dorsal seta on trochanter I stout and spine-like ; seta ad_1 on femora II–IV relatively stout and spine-like. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	63/24	42/40	45/35	60/32
tibia	68/18	45/33	42/30	57/27
tarsus	123/19	80/25	78/24	110/20

HABITAT : Ants' nests (*Formica* sp.) in the Black Wood of Rannoch, Perthshire, Scotland, and in Europe.

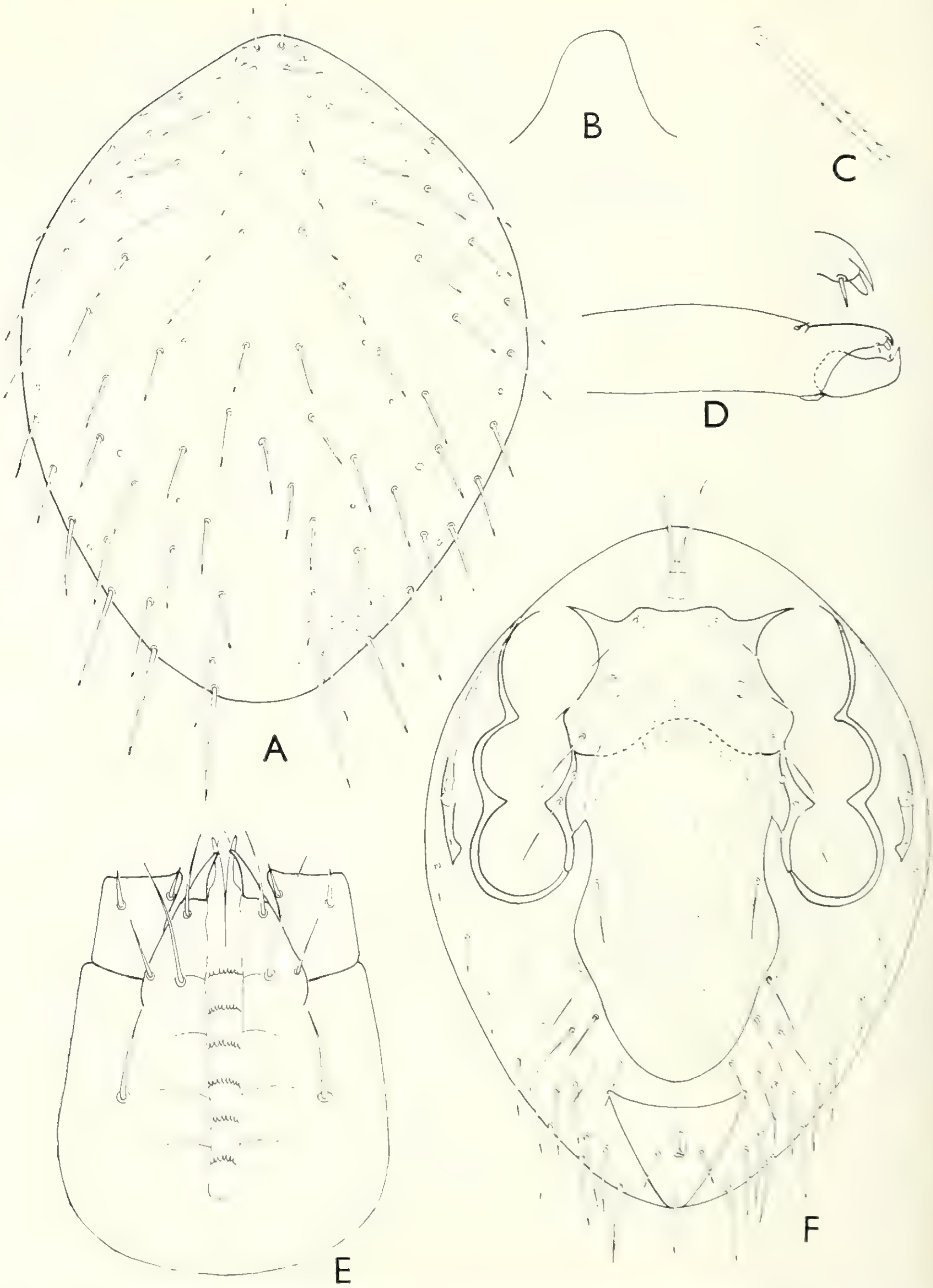


FIG. 36. *Hypoaspis isotricha* (Kolenti), female; dorsum of idiosoma (A); tectum (B); dorsal seta (C); chelicera (D); venter of gnathosoma (E); venter of idiosoma (F).

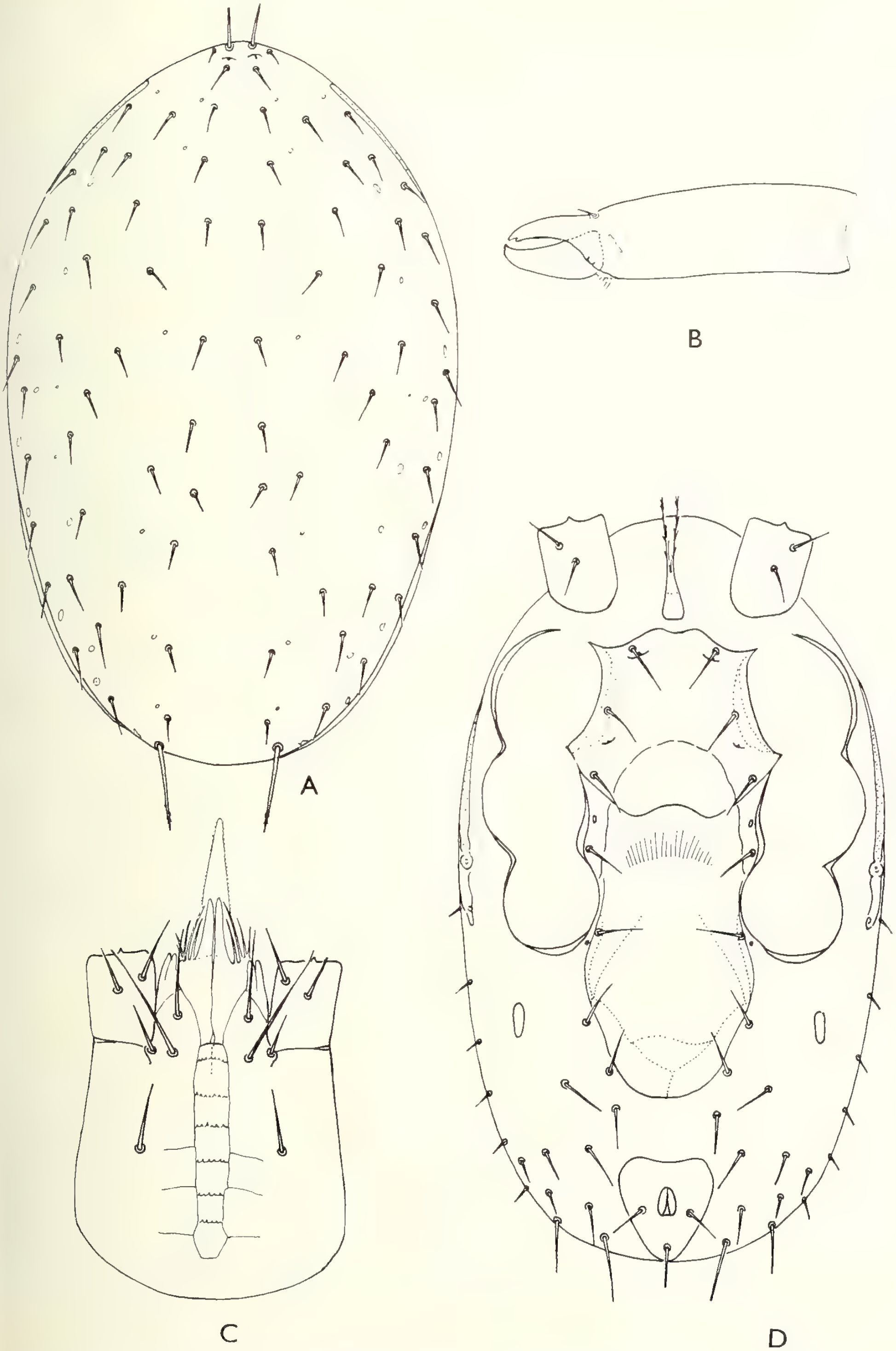


FIG. 37. *Hypoaspis montana* (Berlese), female ; dorsum of idiosoma (A) ; chelicera (B) ; venter of gnathosoma (C) ; venter of idiosoma (D).

Hypoaspis montana (Berlese)

Laelaps (*Oolaelaps*) *montanus* Berlese, 1904, *Redia* **1** : 430.

Female : Chelicera with segment I, 20 μ ; II, 75 μ ; movable digit 21 μ, edentate ; fixed digit unidentate ; pilus dentilis absent, dorsal seta and arthrodial processes present (Text-fig. 37B). Four pairs of gnathosomal setae with *c.s.* about 36 μ apart, *hyp*.2 about 30 μ apart. Deutosternum with six transverse rows of denticles (4–8 denticles per row) ; corniculi horn-like, bifid at tip, about 20 μ long ; internal malae fimbriate (Text-fig. 37C). Tectum capituli with anterior margin smooth. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (468 μ × 312 μ) with 39 pairs of setae distributed as in Text-fig. 37A ; a pair of accessory setae situated between the *J* series. Setae *Z*5 pilose distally and about three times the length of simple seta *J*5. Anterior part of shield " sculptured ", reticulations and striations distinct only in the marginal zone.

Tritosternum with base 20 μ, laciniae 54 μ. Sternal shield (105 μ × 100 μ) with weak striations laterally, bearing three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 50 μ ; between *st*1 and *st*3, 87 μ. Genital shield (110 μ × 95 μ) with genital setae only. Anal shield (60 μ × 57 μ) with paranal setae 24 μ, postanal seta 30 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 37D. Peritremes extend to middle of coxa I ; peritrematal shields free posteriorly.

Chaetotaxy of legs normal. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	63/30	51/36	42/28	60/30
tibia	70/30	45/33	40/26	60/28
tarsus	114/27	78/24	70/24	96/24 approx.

HABITAT : Ants' nest near Canterbury, Kent, 25th April, 1942, coll. Dr. E. Warren. Recorded from nests of *Formica rufa* Linn., *F. fusca* Linn. and *Lasius niger* (Linn.) in Britain and Ireland, and from ants' nests in Europe.

Hypoaspis oophila (Wasman)

Laelaps oophilus Wasman, 1897, *Zool. Anz.* **20** : 172.

Female : Chelicera with movable digit 18 μ long, bidentate ; fixed digit unidentate ; pilus dentilis and dorsal seta short, setiform ; arthrodial processes reduced (Text-fig. 38B). Four pairs of gnathosomal setae with *c.s.* about 54 μ apart, *hyp*.2 about 42 μ apart. Deutosternum with six transverse rows of denticles (5–7 denticles per row) ; corniculi horn-like, 21 μ long ; internal malae weakly serrate basally (Text-fig. 38D). Tectum capituli with smooth margin (Text-fig. 38C). Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (600 μ × 438 μ) with 39 pairs of setae distributed as in Text-fig. 38A ;

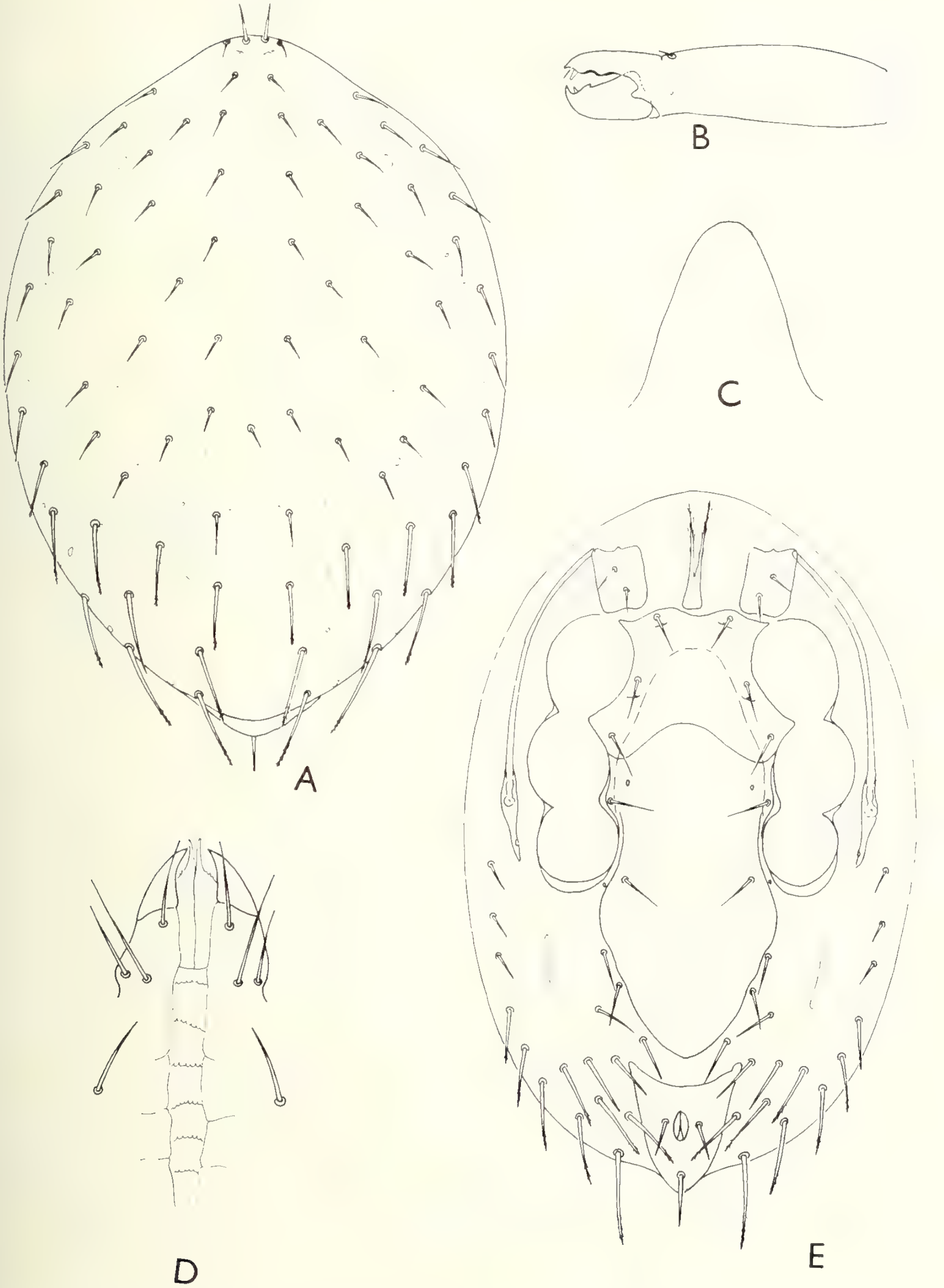


FIG. 38. *Hypoaspis oophila* (Wasman), female; dorsum of idiosoma (A); chelicera (B); tectum capituli (C); deutosternum and hypostome (D); venter of idiosoma (E).

a single accessory seta present between the *J* series. Setae markedly unequal in length ; *J*4–5, *Z*3–5 and *S*2–5 pilose distally and considerably longer than the remaining simple setae. Surface of shield reticulated.

Tritosternum with base 36 μ, laciniae 60 μ. Sternal shield (102 $\mu \times$ 117 μ) with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 66 μ ; between *st*1 and *st*3, 110 μ. Genital shield (153 $\mu \times$ 140 μ) tapers posteriorly and bears a pair of genital setae only. Anal shield (80 $\mu \times$ 72 μ ; maximum width 96 μ) with paranal setae 33 μ, postanal seta 48 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 38E. Peritremes extend to a point above coxae I ; peritrematal shields free posteriorly.

Chaetotaxy of legs normal. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	54/21	40/45	38/42	48/36
tibia	60/18	36/33	33/38	48/30
tarsus	108/21	80/24	84/24	102/24

HABITAT : Nests of *Formica fusca* Linn., Leeds, England (Hull Collection) ; recorded from several *Formica* species in Britain and Europe.

Hypoaspis astronomica (Koch)

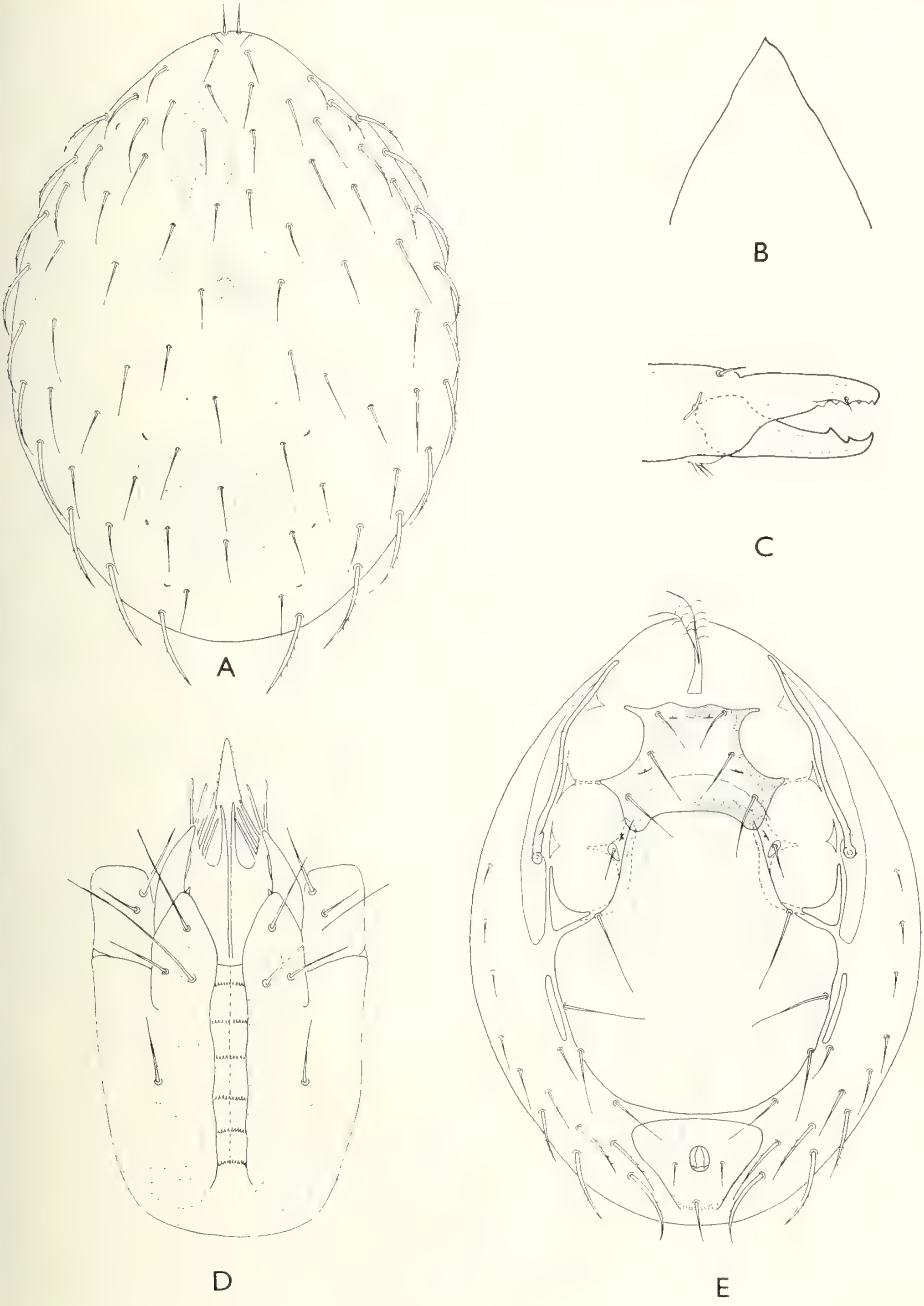
Iphis astronomicus Koch, 1839, *Deutschl. C.M.A.* fasc. 27, t. 18.
Laelaspis ovatus Willmann, 1951, *S.B. Akad. Wiss. Wien.* **160** : 115, fig. 7 (**syn. nov.**).

Female : Chelicera with segment I, 45 μ ; II, 150 μ ; movable digit 36 μ, bidentate ; fixed digit with about five teeth, pilus dentilis minute, setiform (Text-fig. 39C). Four pairs of gnathosomal setae with *c.s.* about 45 μ apart ; *hyp.*2 about 36 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 30 μ long ; hypostome with about six pairs of finger-like processes (Text-fig. 39D). Tectum capituli with anterior margin apparently smooth (Text-fig .39B). Salivary styli slender, reaching tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (552 $\mu \times$ 396 μ) with 39 pairs of setae and three unpaired accessory setae (Text-fig. 39A). Setae of the *s* and *S* series and seta *Z*5 relatively long, stout and barbed. Surface of shield reticulate.

Tritosternum with base 20 μ, laciniae 72 μ. Sternal shield (96 $\mu \times$ 96 μ) with heavily sclerotized margins ; with three pairs of setae and two pairs of pores ; metasternal setae on small shields, associated pores on cuticle. Between *st*1, 63 μ ; between *st*1 and *st*3, 84 μ. Genito-ventral shield (186 $\mu \times$ 186 μ) greatly expanded behind coxae IV, with three pairs of setae. Anal shield (78 $\mu \times$ 102 μ) with maximum width at anterior margin 126 μ ; paranal setae 21 μ, postanal seta 33 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 39E. Peritreme ex-

FIG. 39. *Hypoaspis astronomica* (Koch), female ; dorsum of idiosoma (A) ; tectum (B) ; chelicera (C) ; venter of gnathosoma (D) ; venter of idiosoma (E).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tends to anterior margin of coxa I ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs normal. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	70/27	48/33	42/33	60/30
tibia	75/24	48/33	40/27	60/27
tarsus	126/20	93/27	93/24	130/24

HABITAT : Ants' nests in Britain (Cornwall) and in Germany.

Hypoaspis equitans (Michael)

Laelaps equitans Michael, 1891. *Proc. zool. Soc. Lond.* : 649.

Female : Chelicera with segment I, 42 μ ; II, 126 μ ; movable digit 42 μ ; both digits virtually edentate with two slight irregularities on the internal margin ; pilus dentilis short, setiform (Text-fig. 40B). Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp*.2 about 40 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 27 μ long ; internal malae with inner and outer finger-like processes and shorter fimbriae between these. Salivary styli and tectum capituli not clearly visible. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (672 μ × 486 μ) with 39 pairs of setae and six unpaired accessory setae distributed as in Text-fig. 40A. Most of the setae, especially in the opisthonotal region, are long and sinuous. Surface of shield reticulate.

Tritosternum with base 30 μ, lacininae 66 μ. Sternal shield (135 μ × 144 μ) with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between *st*1, 78 μ ; between *st*1 and *st*3, 108 μ. Genito-ventral shield (210 μ × 222 μ) expanded behind coxae IV, with two pairs of setae. Anal shield (126 μ × 105 μ) with maximum width 150 μ at anterior margin ; paranal setae 36 μ, postanal seta 85 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 40C. Peritreme extends beyond posterior margin of coxa I.

Legs with normal chaetotaxy. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	102/40	78/48	72/45	90/40
tibia	120/36	72/42	72/42	93/36
tarsus	198/33	132/30	144/30	180/30

HABITAT : Ants' nests [*Tetramorium caespitum* (Linn.)] in Britain (Cornwall, Lundy Island Berkshire).

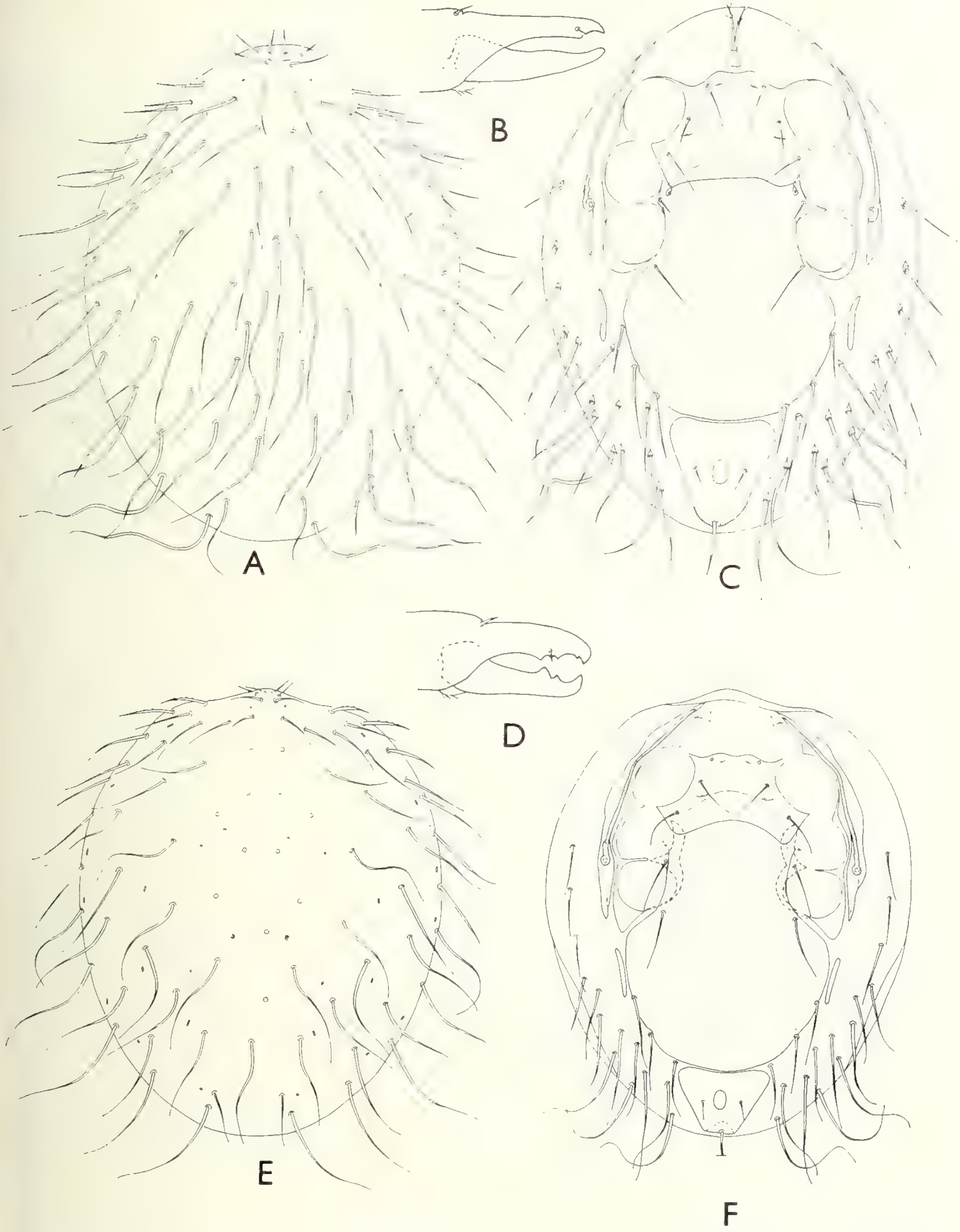


FIG. 40. A–C. *Hypoaspis equitans* (Michael), female ; dorsum of idiosoma (A) ; chelicera (B) ; venter of idiosoma (C). D–F. *Hypoaspis humerata* (Berlese), female ; chelicera (D) ; dorsum of idiosoma (E) ; venter of idiosoma (F).

Hypoaspis humerata (Berlese)

Laelaps (*Laelaspis*) *humeratus* Berlese, 1904, *Redia* **1** : 425, pl. 18, figs. 151–153.

Female : Chelicera with segment II, 110 μ ; movable digit 36 μ, bidentate ; fixed digit tridentate (Text-fig. 40D). No other details of the gnathosomal structure can be described owing to the poor condition of the only available specimen.

Dorsal shield (approximately 600 μ × 490 μ) with 39 pairs of setae distributed as in Text-fig. 40E, and three unpaired accessory setae. Surface of shield reticulate.

Sternal shield (90 μ × 120 μ) with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between *st*1, 63 μ ; between *st*1 and *st*3, 84 μ. Genito-ventral shield (210 μ × 198 μ) expanded behind coxae IV with maximum width 282 μ ; with two pairs of setae, a third pair being just on or off the margin of the shield. Anal shield (84 μ × 90 μ) with maximum width 123 μ at anterior margin ; paranal setae 30 μ long, postanal seta broken. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 40F. Peritreme extends approximately to middle of coxa I ; posterior part of peritrematal shield free.

Legs apparently with normal chaetotaxy, although this cannot be checked on every segment. Legs rather short and stumpy. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	45/27	40/54	33/45	45/42
tibia	48/24	36/42	33/42	45/36
tarsus	100/24	75/30	75/33	102/30

HABITAT : Found in ants' nests [*Tetramorium caespitum* (Linn.)] in Britain (Cornwall) and in Luxemburg.

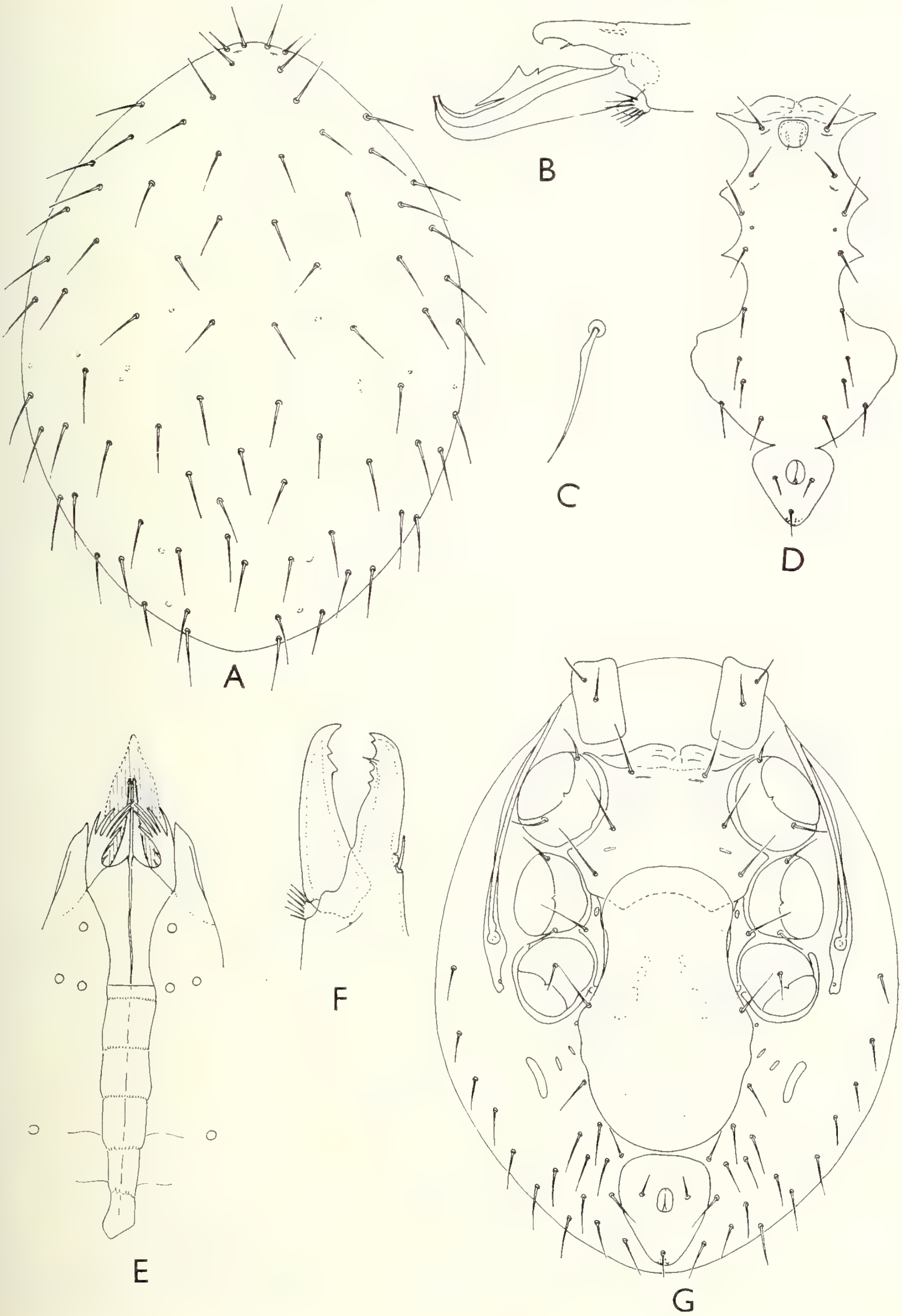
Hypoaspis acuta (Michael)

Laelaps acuta Michael, 1891, *Proc. zool. Soc. Lond.* : 652.

Female : Chelicera with segment I, 60 μ ; II, 177 μ ; movable digit 57 μ, bidentate ; fixed digit with four teeth ; pilus dentilis short, setiform ; dorsal seta present (Text-fig. 41F). Four pairs of gnathosomal setae with *c.s.* about 66 μ apart ; *hyp.2* about 48 μ apart. Deutosternum with five transverse rows of denticles, each row multidenticulate ; corniculi horn-like, 40 μ long ; internal malae fimbriate (Text-fig. 41E). Tectum capituli with anterior margin apparently smooth. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (720 μ × 468 μ) with 37 pairs of setae distributed as in Text-fig. 41A ; setae *z*3 and *r*1 lacking on the podonotal region ; about four accessory setae present on the opisthonotal region between the *J* series. Setae inflated sub-basally (Text-fig. 41C).

FIG. 41. *Hypoaspis acuta* (Michael). A. Dorsum of idiosoma of female ; B. chelicera of male ; C. dorsal seta *z*5 of female ; D. holoventral shield of male ; E. deutosternum and hypostome of female ; F. chelicera of female ; G. venter of idiosoma of female.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Tritosternum with base 48 μ, laciniae 90 μ. Sternal shield (140 μ × 150 μ) granular, reticulated laterally, bearing three pairs of setae and two pairs of pores. Metasternal setae and pores situated on cuticle overlying the endopodal shields. Between *st*1, 80 μ ; between *st*1 and *st*3, 129 μ. Genital shield (168 μ × 170 μ) flask-shaped with genital setae only. Anal shield (105 μ × 100 μ) pear-shaped, paranal setae 36 μ, postanal seta 48 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 41G. Peritremes extend to anterior third of coxae I ; pertrematal shields free posteriorly.

Chaetotaxy of legs normal except genu IV which has two postero-lateral setae $(2-\frac{2}{1}, \frac{3}{0}-2)$. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	108/36	75/48	70/40	114/40
tibia	120/30	78/40	72/36	117/36
tarsus	192/30	140/33	147/32	228/33

Male : Chelicera with segment I, 48 μ ; II, 123 μ ; movable digit dentate, partially fused with a grooved spermadactyl which measures 60 μ in length from the base of the movable digit (Text-fig. 41B). Pilus dentilis and dorsal seta as in female. Four pairs of gnathosomal setae with *c.s.* about 54 μ apart ; *hyp.2* about 45 μ apart. Deutosternum with about four transverse rows of denticles ; corniculi horn-like, 32 μ long ; internal malae fimbriate. Pedipalps and tectum as in female.

Dorsal shield (582 μ × 354 μ) with chaetotaxy as in female. Holoventral shield (450 μ × 108 μ) expanded behind coxae IV, bearing nine pairs of setae excluding the anals (Text-fig. 41D). Between *st*1, 72 μ ; between *st*1 and *st*3, 100 μ. Paranal setae 36 μ, postanal seta 30 μ long. Peritremes extend to middle of coxae I.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	87/33	66/40	57/33	93/33
tibia	102/28	63/36	57/30	99/33
tarsus	162/27	114/30	120/24	186/27

HABITAT : In the nests of *Myrmica scabrinodis* Nylander in Mayo, Ireland, and *Camponotus herculeanus* (Linn.) in Europe.

Hypoaspis myrmecophila (Berlese)

Laelaps myrmecophilus Berlese, 1892, *Acari, Myr. Scorp. Ital.* fasc. 69, no. 2.
Laelaps ovalis (Moniez), Berlese, 1904, *Redia* **1** : 409.

Female : Chelicera with segment I, 150–190 μ ; II, 324–336 μ ; movable digit 135 μ, bidentate ; fixed digit with about nine teeth, pilus dentilis short, setiform (Text-fig. 42E). Four pairs of gnathosomal setae with *c.s.* about 84 μ apart, *hyp.2* about 70 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 98 μ ; internal malae with slender inner and triangular median, pilose lobes, and

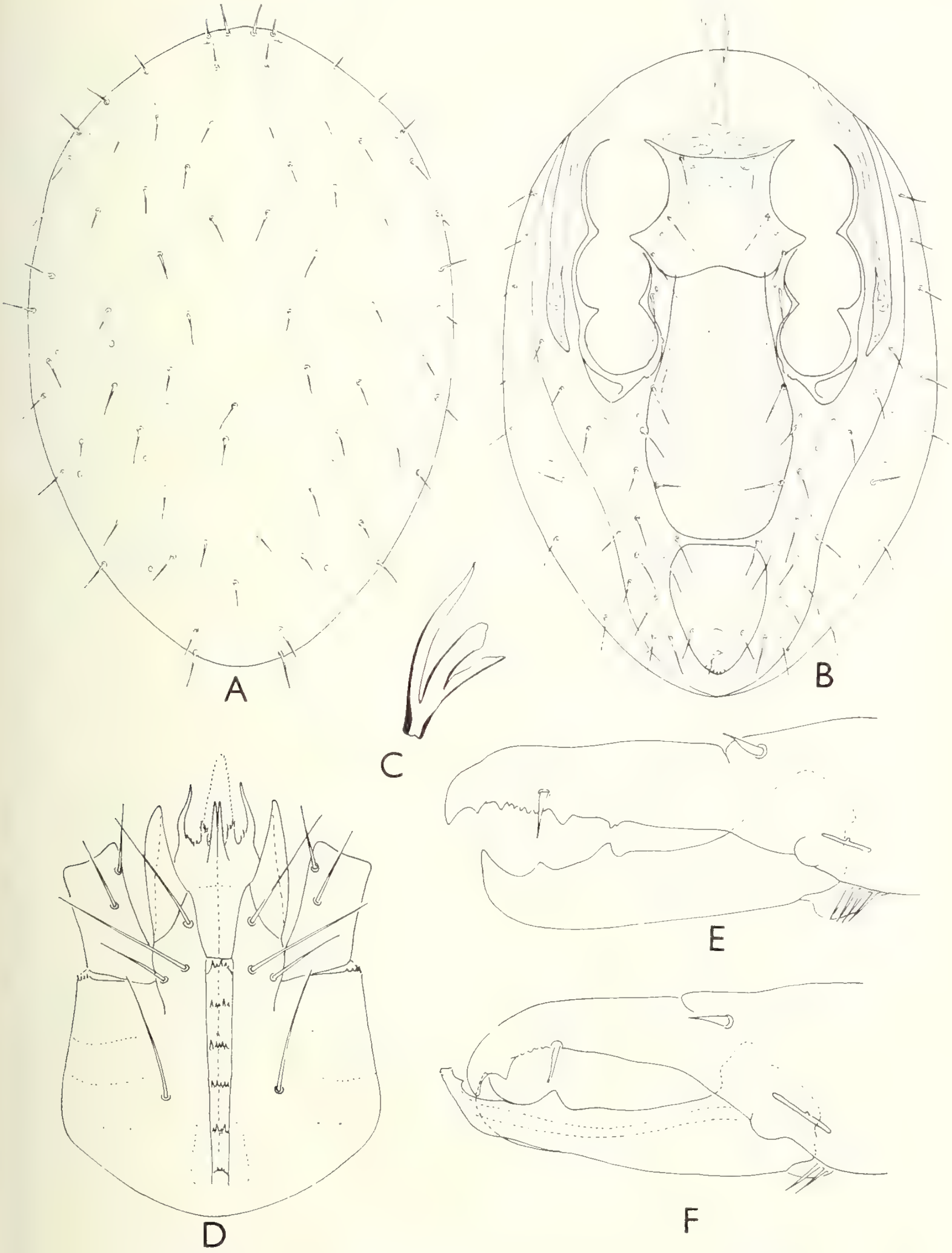


Fig. 42. *Hypoaspis myrmecophila* (Berlese). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. apotele of pedipalp; D. venter of gnathosoma of female; E. chelicera of female; F. chelicera of male.

long, slender, outer lobes (Text-fig. 42D). Tectum capituli with denticulate anterior margin. Salivary styli long, slender, reaching approximately to tips of corniculi. Pedipalp (2–5–6–14) with three-tined apotele (Text-fig. 42C).

Dorsal shield (1,116 $\mu \times 768$ μ) with 41 pairs of slender, simple setae and five unpaired accessory setae (Text-fig. 42A) ; an extra pair of r setae is present in the podonotal region and setae $px1$ are present in the opisthonotal region. Surface of shield granular, with sculpturing anteriorly.

Tritosternum with base 60 μ, laciniae 168 μ ; pre-endopodal shields large, reticulate and granular. Sternal shield (180 $\mu \times 240$ μ) granular, reticulate antero-laterally, with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between $st1$, 126–132 μ ; between $st1$ and $st3$, 180–192 μ. Genito-ventral shield (290 $\mu \times 246$ μ) with one pair of genital and one pair of opisthogastric setae. Anal shield (198 $\mu \times 120$ μ) with maximum width 186 μ ; paranal setae 48 μ ; postanal seta 30 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 42B. Peritreme extends to about posterior third of coxa I ; posterior part of peritrematal shield free.

Legs with normal chaetotaxy. Relatively stout setae present on femur I (pd_{2-3}), tarsus II (ventrals, al_1, pl_1, md), and femur IV (ad_2 and pd_1). Seta pl on genu IV stout and spine-like (Text-fig. 44B). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	192/66	156/90	126/66	180/78
tibia	222/60	144/80	120/66	180/78
tarsus	300/54	228/63	228/54	306/63

Male : Chelicera with segment I, 108 μ ; II, 300 μ ; movable digit 126 μ, unidentate ; spermadactyl 140 μ, a small tooth near its tip ; fixed digit with one large and about five small teeth ; pilus dentilis short, setiform (Text-fig. 42F). Four pairs of gnathosomal setae with $c.s.$ about 78 μ apart, $hyp.2$ about 75 μ apart. Corniculi 90 μ long, internal malae not clearly visible. Deutosternum, salivary styli, tectum capituli and pedipalps as in female.

Dorsal shield (1,080 $\mu \times 756$ μ) as in female. Holoventral shield (816 $\mu \times 216$ μ) with four pairs of setae and three pairs of pores in the sternal region, one pair of genital and five pairs of opisthogastric setae in the genito-ventral region (Text-fig. 44A). Between $st1$, 114 μ ; between $st1$ and $st3$, 195 μ. Paranal setae 60 μ, postanal seta 42 μ. Peritreme extends to posterior margin of coxa I. Posterior part of peritrematal shield free.

Legs with normal chaetotaxy, stout setae as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	180/66	162/90	132/72	192/84
tibia	210/60	150/84	126/66	198/78
tarsus	270/54	220/60	240/54	300/60

HABITAT : Found in ants' nests in Britain (Cornwall, Devon, Wales, Isle of Wight) and Europe.

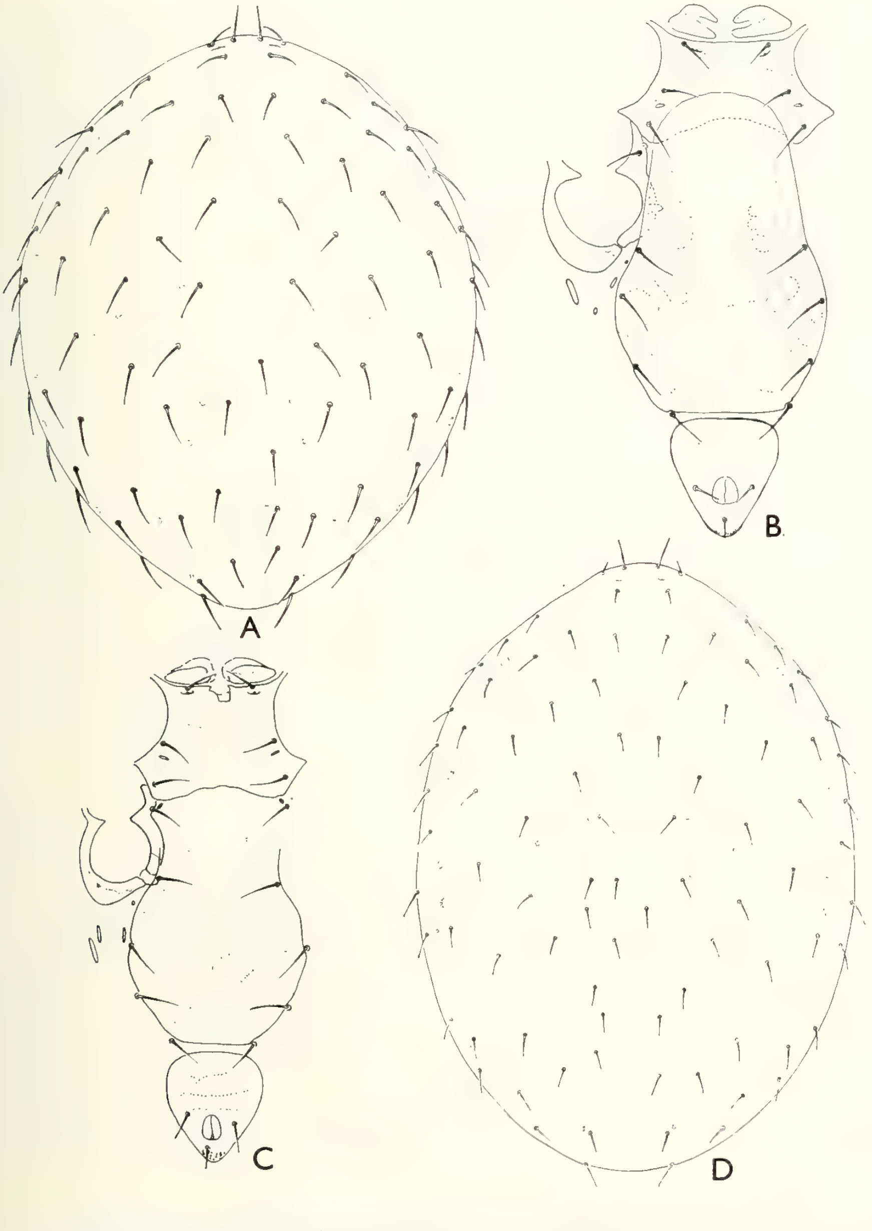


FIG. 43. A–B. *Hypoaspis myrmophila* (Michael), female ; dorsum (A) and venter (B) of idiosoma. C–D. *Hypoaspis laevis* (Michael), female ; venter (C) and dorsum (D) of idiosoma.

Hypoaspis myrmophila (Michael)

Laelaps myrmophila Michael, 1891, *Proc. zool. Soc. Lond.* : 649.

Female : Chelicera with segment I, 90 μ ; II, 246 μ ; movable digit 105 μ, bidentate ; fixed digit with four conspicuous teeth and a row of 3–5 tiny teeth ; pilus dentilis and dorsal seta normal. Four pairs of gnathosomal setae with *c.s.* about 66 μ apart, *hyp.*2 about 63 μ apart. Deutosternum with six transverse rows of denticles, each row multidenticulate ; corniculi horn-like, 63 μ long ; internal malae as in *H. myrmecophila*, but middle process almost as long as inner, and outer process forked at tip. Tectum capituli with anterior margin serrated. Pedipalp (2-5-6-14) with three-tined apotele.

Dorsal shield (696 μ × 528 μ) with 40 pairs of setae and seven unpaired accessories distributed as in Text-fig. 43A ; an extra pair of *r* setae is present in the podonotal region.

Tritosternum with base 40 μ, laciniae 114 μ. Pre-endopodal shields present. Sternal shield (96 μ × 180 μ) reticulated antero-laterally, with three pairs of setae and two pairs of pores ; metasternal setae and associated pores situated over the endopodal shields. Between *st*1, 99 μ ; between *st*1 and *st*3, 105 μ. Genito-ventral shield (210 μ × 190 μ) reticulated, bearing a pair of genital and two pairs of opisthogastric setae. Anal shield (114 μ × 99 μ ; maximum width 138 μ) with the usual three setae. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 43B. Peritreme extends to about middle of coxa I ; posterior part of peritrematal shield free.

Legs with normal chaetotaxy. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	105/48	96/60	66/42	114/48
tibia	126/45	90/57	69/42	114/48
tarsus	198/42	150/42	140/36	180/38

Male : Chelicera with segment I, 78 μ ; II, 210 μ ; movable digit 84 μ, unidentate ; spermadactyl relatively short, 102 μ from base of movable digit ; fixed digit with one large and two small teeth (Text-fig. 44D). Pilus dentilis and dorsal seta normal. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 57 μ apart. Corniculi horn-like, 54 μ long ; internal malae pilose. Deutosternum, tectum and pedipalps as in female.

Dorsal shield (612 μ × 420 μ) with chaetotaxy as in female. Pre-endopodal shields present. Holoventral shield (516 μ × 144 μ) with ten pairs of setae, excluding the anals (Text-fig. 44E). Between *st*1, 87 μ ; between *st*1 and *st*3, 117 μ. Peritreme extends to about middle of coxa I.

Legs with normal chaetotaxy. Genu and tibia II with seta *pv* stout ; tarsus II with ventral setae and al_1 and pl_1 stout. Length/width (in μ) of leg segments :

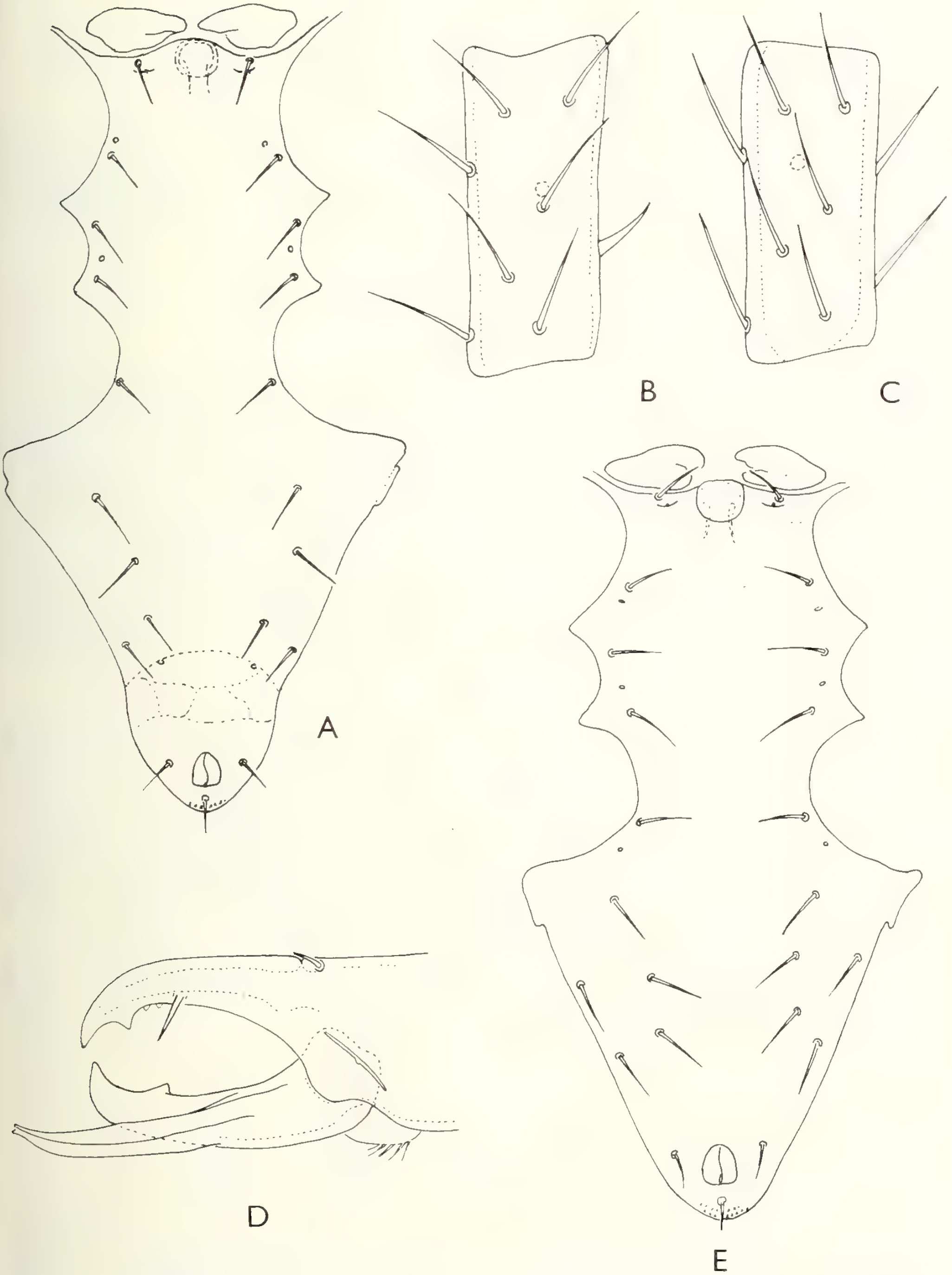


FIG. 44. A. *Hypoaspis myrmecophila* (Berlese), holoventral shield of male ; B. *H. myrmecophila*, genu IV of female ; C. *Hypoaspis laevis* (Michael), genu IV of female ; D. *Hypoaspis myrmophila* (Michael), chelicera of male ; E. *H. myrmophila*, holoventral shield of male.

	I	II	III	IV
genu	96/45	90/57	66/38	99/45
tibia	111/38	84/51	63/39	105/45
tarsus	180/36	138/38	126/32	162/36

HABITAT : The nests of ants [*Lasius mixtus* Nylander, *L. flavus* (Fabr.), *Formica fusca* Linn., *Tetramorium caespitum* (Linn.)] in Cornwall, Surrey and Northumberland ; ants' nests in Corsica.

Hypoaspis laevis (Michael)

Laelaps laevis Michael, 1891, *Proc. zool. Soc. Lond.* : 648.

Female : Chelicera with segment I, 90 μ ; II, 324 μ ; movable digit 130 μ, bidentate ; fixed digit with three prominent teeth and a row of about four small ones. Pilus dentilis and dorsal seta short, setiform. Four pairs of gnathosomal setae with *c.s.* about 102 μ apart, *hyp.*2 about 78 μ apart. Deutosternum with five transverse rows of denticles (4–9 denticles per row). Corniculi horn-like, 80 μ long ; internal malae comprise pilose outer, middle and inner processes. Tectum capituli with anterior margin denticulate. Pedipalp (2–5–6–14) with three-tined apotele.

Dorsal shield (1,140 μ × 770 μ) with 41 pairs of setae and about six accessories distributed as in Text-fig. 43D ; an additional pair of *r* setae is present on the podonotal region and an extra pair of *px* setae on the opisthonotal region. Surface of shield granular with some striations near the margin.

Tritosternum with laciniae about 2½ times the length of the base. Pre-endopodal shields present. Sternal shield (204 μ × 246 μ) reticulated antero-laterally, with three pairs of setae and two pairs of pores ; metasternal setae situated over the endopodal shields. Between *st*1, 70 μ ; between *st*1 and *st*3, 192 μ. Genito-ventral shield (312 μ × 237 μ) reticulated, with one pair of genital and two pairs of opisthogastric setae. Anal shield (186 μ × 132 μ ; maximum width 195 μ) with paranal setae 45 μ, postanal seta 21 μ long. Sclerotization of opisthogaster as in Text-fig. 43C. Peritreme extends at least to anterior margin of coxa I ; peritrematal shield fused anteriorly with dorsal shield, posterior part free.

Chaetotaxy of legs normal except genu IV which has two postero-lateral setae (2—$\frac{2}{1}$, $\frac{3}{0}$—2) as in Text-fig. 44C. Tarsus II with several stout setae (av_1, pv_1, al_1, pl_1). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	180/66	144/87	126/66	180/75
tibia	222/57	150/80	126/60	198/75
tarsus	306/54	228/57	240/48	318/57

HABITAT : Nests of ants [*Tetramorium caespitum* (Linn.)] in Cornwall and in Austria.

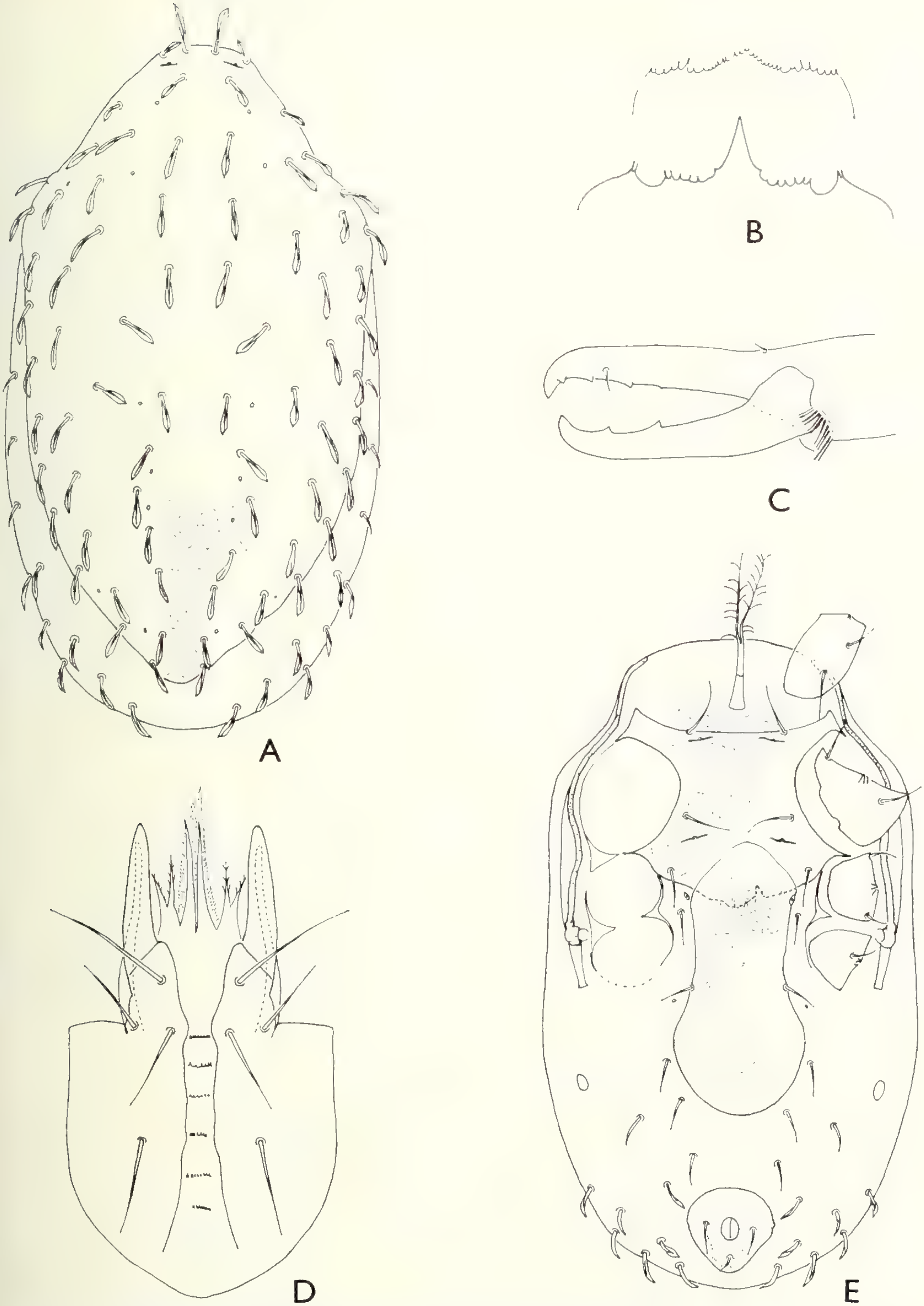


FIG. 45. *Hypoaspis miles* (Berlese), female ; dorsum of idiosoma (A) ; tecta capituli (B) ; chelicera (C) ; venter of gnathosoma (D) ; venter of idiosoma (E).

Hypoaspis miles (Berlese)

Laelaps (*Iphis*) *miles* Berlese, 1892, *Acari, Myr. Scorp. Ital.* fasc. 63, no. 9.
Cosmolaelaps gurabensis Fox, 1946, *J. Parasit.* **32** : 449, fig. 1.
Bregetova, 1956, *Opred. Faune SSSR.* **61** : 75, figs. (**syn. nov.**).

Female : Chelicera with segment I, 96 μ ; II, 216 μ ; movable digit 130 μ long, bidentate ; fixed digit with about four teeth ; pilus dentilis short, setiform (Text-fig. 45C). Four pairs of gnathosomal setae with *c.s.* about 63 μ and *hyp.2* about 66 μ apart. Deutosternum with six transverse rows of denticles ; corniculi 90 μ long ; outer processes of internal malae fringed (Text-fig. 45D). Tectum capituli with denticulate anterior margin (Text-fig. 45B). Salivary styli conspicuous, almost reaching tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (648 μ × 348 μ) with 37 pairs of leaf-like setae distributed as in Text-fig. 45A ; setae *px*2 and *px*3 absent. Surface of shield reticulated ; no hypertrichy ; seven pairs of *R* setae on the cuticle.

Tritosternum with base 60 μ, laciniae 96 μ. Sternal shield (180 μ × 138 μ) extending almost to posterior margin of coxa III, with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 96 μ ; between *st*1 and *st*3, 144 μ. Genital shield flask-shaped (135 μ × 102 μ), with one pair of setae. Anal shield (72 μ × 87 μ) with paranal setae about 24 μ, postanal seta about 15 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 45E. Peritreme extends nearly to anterior margin of coxa I ; peritrematal shields free anteriorly and posteriorly.

Legs with normal chaetotaxy. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	87/30	84/50	60/33	93/36
tibia	93/24	78/48	60/33	96/36
tarsus	170/27	144/36	135/30	186/30

HABITAT : Found in decaying oat spillage at Leith, Scotland. Recorded in the literature from a variety of rodents and their nests in Europe, the U.S.S.R. and the U.S.A.

Hypoaspis oblonga (Halbert)

Laelaps (*Hypoaspis*) *oblongus* Halbert, 1915, *Proc. R. Irish Acad.* **31** : 70.
Pseudoparasitus angulatus Berlese, 1917, *Redia* **12** : 164 (**syn. nov.**).
Pseudoparasitus (*Alloparasitus*) *angulatus* Berlese, 1921, *Redia* **14** : 169.

Female : Chelicera with segment I, 60 μ ; II, 162 μ ; movable digit 68 μ, bidentate ; fixed digit with about six teeth (Text-fig. 46B) ; pilus dentilis and dorsal seta short, setiform. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.2* about 40 μ apart. Deutosternum with six transverse rows of denticles (4–6 denticles per row). Corniculi horn-like, 42 μ long ; internal malae fimbriate (Text-fig. 46F).

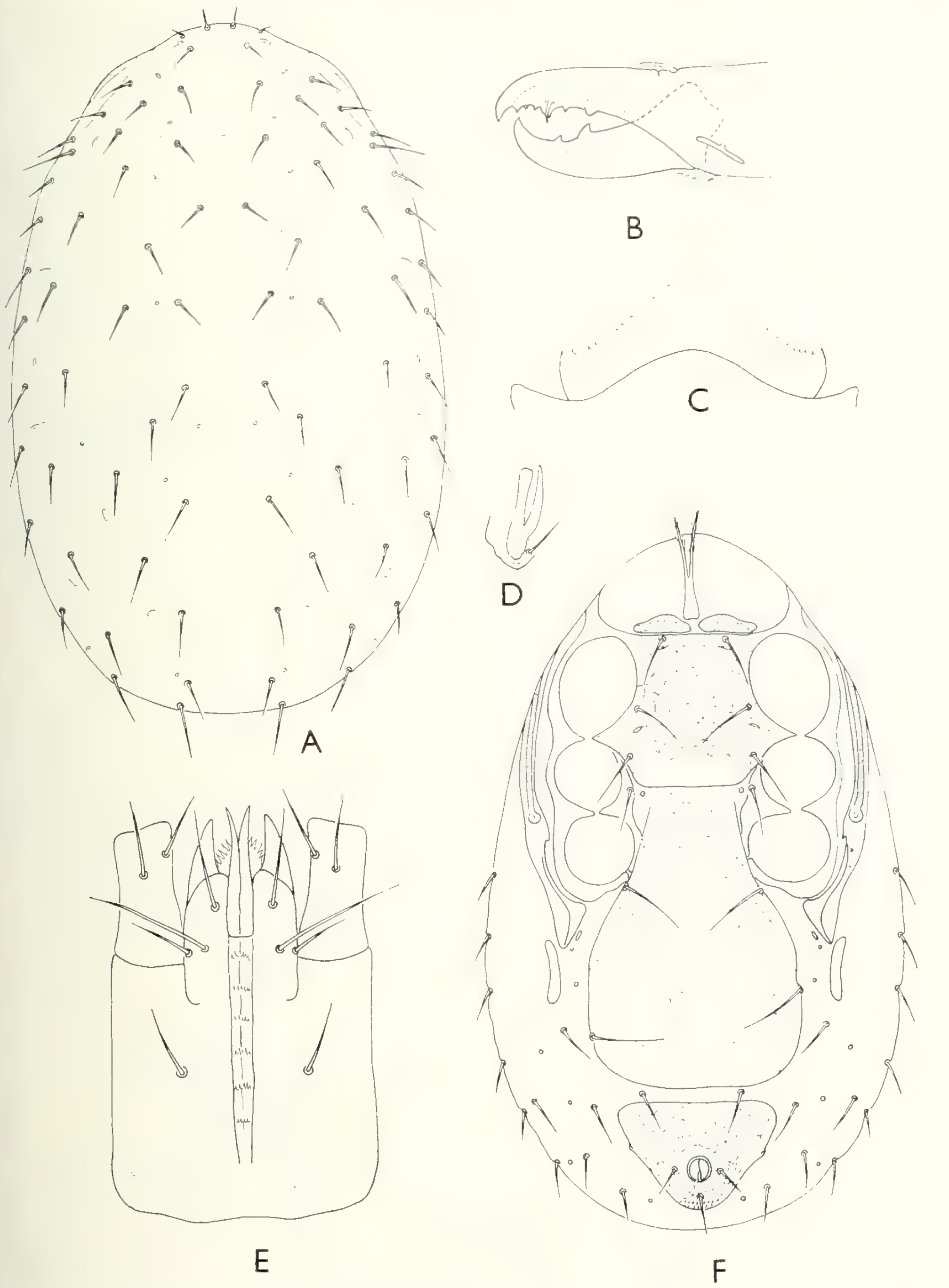


FIG. 46. *Hypoaspis oblonga* (Halbert), female ; dorsum of idiosoma (A) ; chelicera (B) ; tectum capituli (C) ; apotele of pedipalp (D) ; venter of gnathosoma (E) ; venter of idiosoma (F).

Tectum capituli with anterior margin denticulate (Text-fig. 46C). Pedipalp (2–5–6–14) with two-tined apotele (Text-fig. 46D).

Dorsal shield (684 μ × 408 μ) with 39 pairs of setae distributed as in Text-fig. 46A; no hypertrichy. Surface of shield reticulated.

Tritosternum bipartite; pre-endopodal shields present. Sternal shield (150 μ × 132 μ) reticulated, with three pairs of setae and two pairs of pores; metasternals free with associated pores. Between *st1*, 70 μ; between *st1* and *st3*, 120 μ. Genito-ventral shield (204 μ × 144 μ) expanded behind coxae IV and bearing a pair of genital and a pair of opisthogastric setae. Anal shield (100 μ × 100 μ; maximum width 156 μ); paranal setae 36 μ long, postanal seta slightly longer. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 46F. Peritreme extends to middle of coxa I; peritrematal shields extend posteriorly well beyond level of coxae IV, free.

Legs with normal chaetotaxy, except genu IV which has only one antero-lateral seta $(1—\frac{2}{1}, \frac{3}{0}—1)$.

HABITAT: Under bark of decayed trees and in moss, in Ireland, Scotland, England (Northumberland) and Europe.

Genus ***PSEUDOPARASITUS*** Oudemans

Pseudoparasitus Oudemans, 1902, *Tijdschr. Ent.* **45** : 29.
Hoplolaelaps Berlese, 1903, *Zool. Anz.* **27** : 14.
Laelapsoides Willmann, 1952, *Veroff. Inst. Meersforsch. Bremerhaven* **1** : 150.
Austrogamasellus Domrow, 1957, *Proc. Linn. Soc. N.S.W.* **81** : 204, (**syn. nov.**).

Type: *Laelaps meridionalis* Canestrini, 1882.

This genus is closely related to *Ololaelaps* Berlese and differs chiefly in the presence of a discrete anal shield in the female. Chelicerae chelate-dentate in the adults with the movable digit bidentate in the female and unidentate in the male. Pilus dentilis and dorsal seta simple; fissures normal. Spermadactyl long, slender, groove directed anteriorly. Chaetotaxy of venter of gnathosoma and pedipalps normal. Apotele three-tined, posterior tine reduced. Deutosternum with six transverse rows of denticles; internal malae strong; corniculi horn-like. Tectum capituli with anterior margin denticulate.

Dorsal shield entire with 39 pairs of setae (posterior accessories present); no unpaired accessory setae in the region of the *J* series. Tritosternum normal, bipartite. Pre-endopodal shields conspicuous. Sternal shield in the female with three pairs of setae and two pairs of pores. Genito-ventral shield large with four or more pairs of setae of which two pairs are widely removed from its lateral margins. Anal shield free, paranals at level of anterior margin of anus. Podal shields posterior to coxae IV large, not fused with the peritrematal shield. Male with holoventral shield; peritrematal shields free posteriorly.

Leg chaetotaxy normal, seta av_1 on femur II spine-like in the female, spur-like in the male. Coxa II without distinct anterior spine. Ambulacra with paired claws.

We have not studied the immature stages of this genus.

The females of the two British representatives of *Pseudoparasitus* may be readily distinguished by the size and chaetotaxy of the genito-ventral shield, *P. centralis* having five pairs of setae on the shield and *P. dentatus* four pairs. *P. centralis* may be a synonym of *P. meridionalis*, but we are unable to reach a definite conclusion on this since the type material of *meridionalis* appears to be lost.

Pseudoparasitus centralis Berlese

Pseudoparasitus centralis Berlese, 1921, *Redia* **14** : 167.

Female : Chelicera with segment I, 66 μ ; II, 162 μ ; movable digit 66 μ, bidentate ; fixed digit unidentate ; pilus dentilis short, setiform (Text-fig. 47D). Four pairs of gnathosomal setae with *c.s.* about 45 μ apart ; *hyp.*2 about 42 μ apart. Deutosternum with six transverse rows of denticles (1–3 per row) ; corniculi 40 μ long ; internal malae finger-like and denticulate (Text-fig. 47F). Tectum capituli with denticulate anterior margin. Salivary styli do not quite reach tips of corniculi. Pedipalp (2–5–6–14) with three-tined apotele.

Dorsal shield (588 μ × 420 μ) with 39 pairs of setae distributed as in Text-fig. 47A. Surface of shield reticulate and granular ; no hypertrichy.

Tritosternum with base 27 μ, laciniae about 78 μ. Sternal shield (126 μ × 114 μ) extends to posterior margin of coxa III, with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 54 μ ; between *st*1 and *st*3, 99 μ. Genital shield (180 μ × 138 μ) flask-shaped, expanded behind coxae IV, with truncate posterior margin, bearing five pairs of setae. Between *gen.*, 120 μ ; between *Jv*2, 114 μ. Anal shield (96 μ × 105 μ) with a straight anterior margin measuring 180 μ. Paranal setae 30 μ, postanal seta 10 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 47B. Peritreme extends to anterior part of coxa II ; peritrematal shield fused anteriorly with dorsal shield, free posteriorly.

Legs with normal chaetotaxy. Setae av_1 on femur II and pd_1 on femur IV stout and spine-like. Ventral setae on tarsus II stout, pointed. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	75/33	69/45	45/33	63/32
tibia	81/27	57/42	42/35	66/32
tarsus	132/24	96/32	90/28	120/30

Male : Chelicera with segment I, 54 μ ; II, 132 μ ; movable digit 54 μ, unidentate ; spermadactyl as in Text-fig. 47C ; fixed digit bidentate, pilus dentilis slender, setiform. Four pairs of gnathosomal setae with distance between *c.s.* equal to that between *hyp.*2 (42 μ). Deutosternum with six transverse rows of denticles (2–4 per row) ; corniculi 30 μ long. Internal malae elongate, triangular, pilose. Tectum and pedipalps as in female.

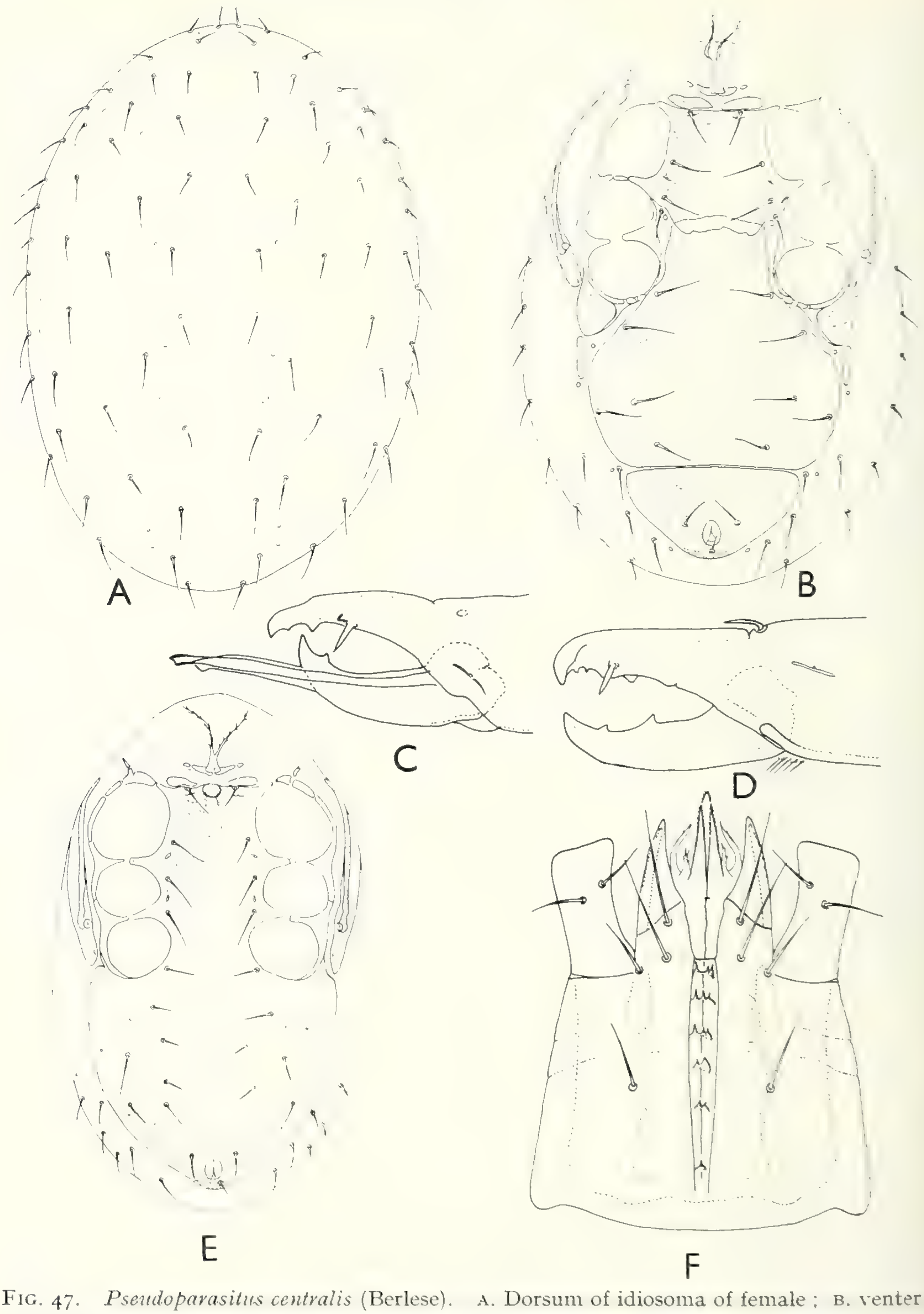


FIG. 47. *Pseudoparasitus centralis* (Berlese). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. chelicera of male; D. chelicera of female; E. venter of idiosoma of male; F. venter of gnathosoma of female.

Dorsal shield (495 μ × 300 μ) with 39 pairs of setae distributed as in female. Tritosternum with base 21 μ, laciniae 63 μ. Holoventral shield (390 μ × 99 μ) with four pairs of setae and three pairs of pores in the sternal region, six pairs of setae in the genito-ventral region. Between *st1*, 45 μ; between *st1* and *st3*, 90 μ. Paranal setae 24 μ, postanal seta 12 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 47E. Peritreme extends nearly to anterior margin of coxa II ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs normal. Femur I with setae ad_2 and pd_3 short, stout and spine-like ; femur II with seta av_1 a stout spine ; genu II with seta *pv* inflated basally ; femur IV with seta pd_3 inflated. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	69/27	66/45	42/30	60/36
tibia	72/27	54/42	40/32	60/40
tarsus	120/22	84/30	84/24	114/30

HABITAT : Free-living in litter under deciduous trees etc. in Britain and Europe.

Pseudoparasitus dentatus (Halbert)

Laelaps dentatus Halbert, 1920, *Proc. R. Irish Acad.* **25** : 123.

Female : Chelicera with segment I, 54 μ II, 162 μ ; movable digit 70 μ, bidentate ; fixed digit with four teeth ; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 48 μ apart, *hyp.*2 42–45 μ apart. Deutosternum with six transvere rows of denticles (5–7 per row) ; corniculi 45–48 μ long. Internal malae as in *P. centralis.* Tectum capituli with denticulate anterior margin. Pedipalp (2–5–6–14) with three-tined apotele.

Dorsal shield (564–678 μ × 348–360 μ) with 39 pairs of setae distributed as in Text-fig. 48A. Surface of shield reticulate ; no hypertrichy.

Tritosternum with base 33 μ, laciniae 81 μ. Sternal shield (150–180 μ × 114–120 μ) with convex posterior margin reaching nearly to posterior margin of coxa III ; with three pairs of setae and two pairs of pores, the second pair small and circular ; metasternal setae free with associated pores. Between *st1*, 66–72 μ ; between *st1* and *st3*, 108–132 μ. Genital shield (192–216 μ × 105 μ) flask-shaped with four pairs of setae ; between *gen.*, 102 μ ; between *Jv2*, 84 μ. Anal shield (60–68 μ × 75–90 μ) with maximum width (123–170 μ) at anterior margin ; paranal setae 30–40 μ, postanal seta 18–30 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 48B. Peritreme extends to about the anterior fourth of coxa II ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Legs with normal chaetotaxy. Femur II with seta av_1 stout. Femur IV with seta *pd*, stout, spine-like. Tarsus II has setae av_1, av_2, pv_1, pv_2, pl_1 and *mv* all stout basally with fine tips. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	80/30	75/40	45/30	72/36
tibia	87/30	60/42	45/30	72/33
tarsus	138/27	87/32	90/27	105/30

HABITAT : Free-living (in tidal debris, moss under *Calluna*, humus under deciduous trees) in Britain, Ireland and the Channel Islands.

Genus ***OLOLAELAPS*** Berlese

Hypoaspis Berlese, 1903, *Zool. Anz.* **27** : 14 (non *Hypoaspis* Canestrini).
Ololaelaps Berlese, 1904, *Redia* **1** : 260.
Pristolaelaps Womersley, 1956, *J. Linn. Soc. Lond. Zool.* **42** : 511.

Type : *Hypoaspis venetus* Berlese, 1903.

Medium to heavily sclerotized mites. Chelicerae chelate-dentate ; movable digit bidentate in the female, unidentate in the male ; spermadactyl groove straight or

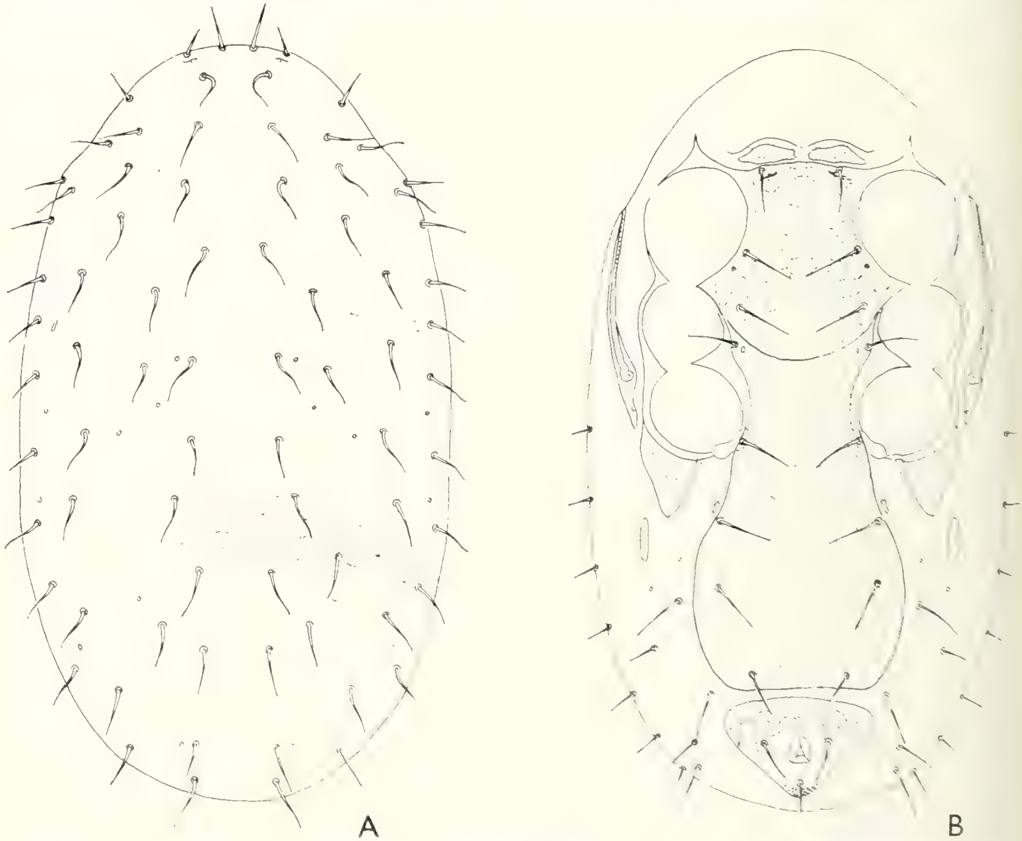


FIG. 48. *Pseudoparasitus dentatus* (Halbert), female ; dorsum (A) and venter (B) of idiosoma.

sinuous. Pilus dentilis and dorsal seta simple, fissures normal. Chaetotaxy of venter of gnathosoma and pedipalps normal; apotele three-tined, posterior tine reduced. Deutosternum with six transverse rows of denticles. Internal malae well-developed; corniculi horn-like. Tectum capituli with rounded, minutely denticulate anterior margin.

Dorsal surface of idiosoma completely covered by an entire shield bearing 37 (*z*1 and *z*3 lacking), 38 (*z*3 lacking) or 39 pairs of fine, simple, setae. Unpaired accessory setae may be present in the region of the *J* series.

Tritosternum normal, bipartite. Pre-endopodal shields conspicuous. Sterno-metasternal shield in the female with four pairs of setae and three pairs of pores. Genito-ventro-anal shield large, bearing four to six pairs of setae excluding the anals, and free or fused by way of the metapodal shields with the peritrematal shields. Male with holoventral shield free or fused with the peritrematal shields. Podal shields strongly developed behind coxae IV.

Segmental chaetotaxy of the legs normal.

Two groups of species appear to be represented within the genus, namely, the *veneta* group in which the peritrematal shields are fused by way of the metapodal shields with the genito-ventral shield of the female, the spermathecal ducts are heavily sclerotized and conspicuous and the spermadactyl groove is sinuous, and the *placentula* group in which the peritrematal shields are free posteriorly in the female, there are no distinct spermathecal ducts and the spermadactyl groove is straight. There is also a tendency in the *veneta* group towards hypotrichy of the podonotum in the adult.

Three species are represented in the British fauna and they appear to favour damp habitats.

Key to Females

1 Paravertical seta (*z*1) absent, dorsal shield with 37 pairs of setae (Text-fig. 50A); spermathecal ducts as in Text-fig. 50E; genito-ventro-anal shield normally with four pairs of setae excluding anals (Text-fig. 50F) **O. sellnicki** Bregetova & Koroleva (p. 231)
– Paravertical setae (*z*1) present, dorsal shield with 38 or 39 pairs of setae . . 2
2 Spermathecal ducts conspicuous (Text-fig. 49C); peritrematal shield fused with the podal and genito-ventro-anal shields (Text-fig. 49B and D); with 38 pairs (*z*3 absent) of relatively short dorsal setae (Text-fig. 49A). **O. veneta** (Berlese) (p. 231)
– Spermathecal duct apparently absent; peritrematal shield free posteriorly (Text-fig. 52F); with 39 pairs of long, fine, dorsal setae (Text-fig. 52A) **O. placentula** (Berlese) (p. 235)

Key to Males

1 Spermadactyl groove straight (Text-fig. 52B); genu III with seta *pv* modified into a rounded protuberance (Text-fig. 52C); dorsal shield with 39 pairs of setae **O. placentula** (Berlese) (p. 237)
– Spermadactyl groove sinuous (Text-fig. 51B and D); genu III with seta *pv* normal; dorsal shield with 37 or 38 pairs of setae 2
2 Paravertical setae absent . . . . **O. sellnicki** Bregetova & Koroleva (p. 233)
– Paravertical setae present. . . . . **O. veneta** (Berlese)

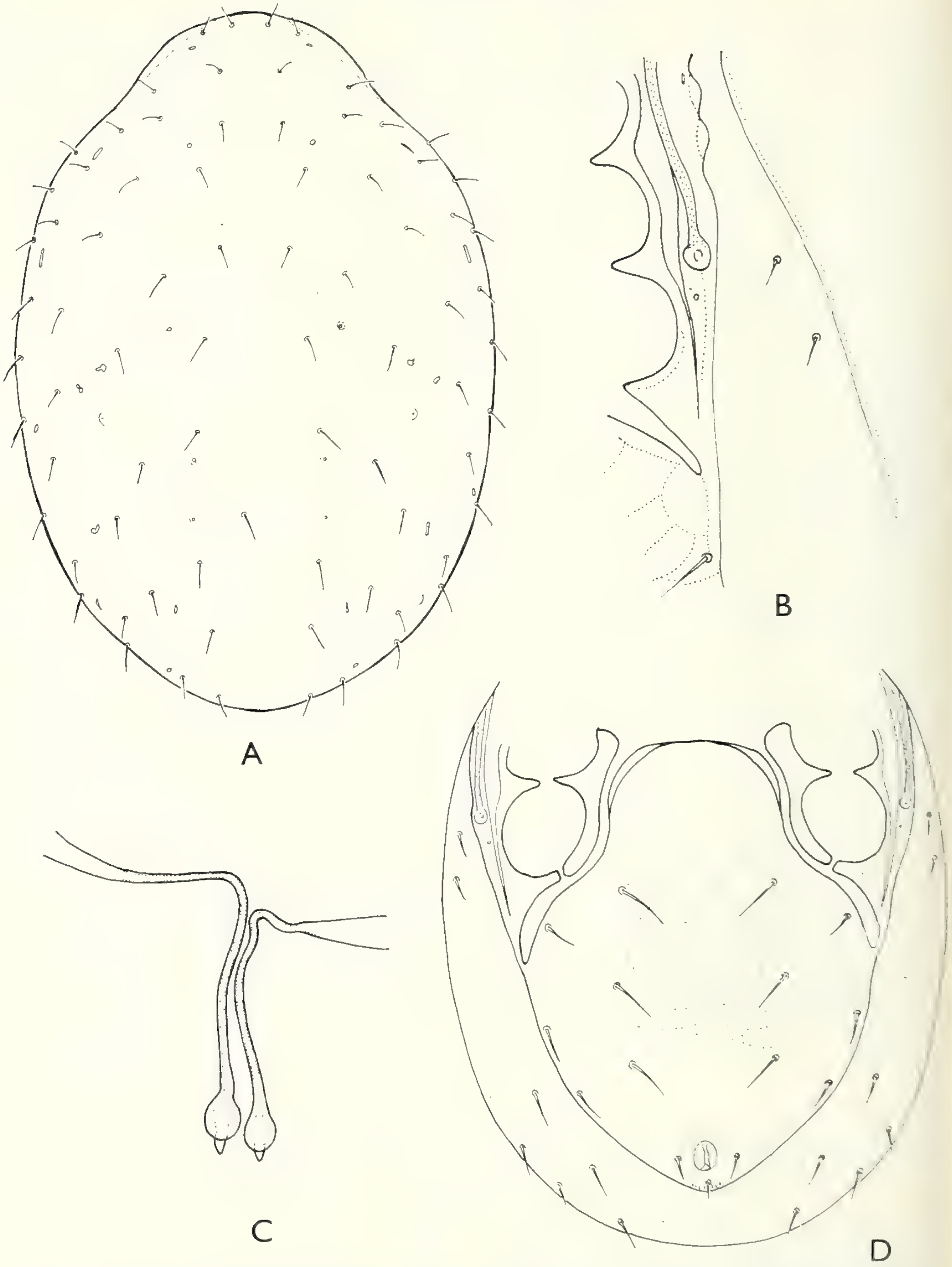


Fig. 49. *Ololaelaps veneta* (Berlese), female; dorsum of idiosoma (A); peritrematal-podal shields in region of coxa IV (B); "spermathecal ducts" (C); genito-ventro-anal shield (D).

Ololaelaps veneta (Berlese)

Laelaps tumidulus (Koch) Berlese, 1889, *Acari, Myr. Scorp. Ital.* fasc. 44, no. 5.
Hypoaspis venetus Berlese, 1903, *Zool. Anz.* **27** : 14 (nom. nov. pro *Laelaps tumidulus* Berlese, 1889 nec Koch).
Ololaelaps venetus Berlese, 1904, *Redia* **1** : 260.
Ololaelaps halaskovae Bregetova & Koroleva, 1964, *Parazit. Sb.* **22** : 81, figs. (**syn. nov.**).

Female : Chelicerae with segment I, 75 μ ; II, 150 μ ; movable digit 87 μ, bidentate ; fixed digit tridentate ; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 57 μ apart ; *hyp*.2 about 48 μ apart. Deutosternum with six transverse rows of denticles (3–6 denticles per row) ; corniculi 45 μ long ; internal malae as in *O. sellnicki*. Tectum capituli with anterior margin finely denticulate. Salivary styli conspicuous. Pedipalp (2–5–6–14) with three-tined apotele.

Dorsal shield (672–804 μ × 444–456 μ) with 38 pairs of relatively short, simple setae distributed as in Text-fig. 49A, seta *z*3 being absent. An unpaired accessory seta is present between the *J* series. Surface of shield granular with sculptured areas in the podonotal region.

Tritosternum with base 30 μ, laciniae 81 μ. Sterno-metasternal shield (102 μ × 132 μ) with four pairs of setae and three pairs of pores. Between *st*1, 66 μ ; between *st*1 and *st*3, 87 μ. Genito-ventro-anal shield (270 μ × 258 μ) with six pairs of setae, excluding the anals. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 49D. Peritreme extends to posterior fourth of coxa I. Peritrematal shield fused with podal shield and with genito-ventro-anal shield (Text-fig. 49B). Spermathecal ducts as in Text-fig. 49C.

Legs with normal chaetotaxy. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	81/36	72/50	54/38	75/40
tibia	87/32	60/45	54/36	75/38
tarsus	153/30	102/34	105/30	135/33

Male : Described and figured by Bregetova & Koroleva (1964).

HABITAT : In moss, Britain and Italy, and in nests of small mammals U.S.S.R.

Ololaelaps sellnicki Bregetova & Koroleva

Ololaelaps haemisphaericus (Koch), Sellnick, 1940, *Göteborgs Vetensk. Samh. Handl.* (5B), **6** (14) : 69, fig. 48.
Ololaelaps sellnicki Bregetova, 1964, *Parazit. Sb.* **22** : 77, figs. (nom. nov. pro *Ololaelaps haemisphaericus* Sellnick, 1940 non Koch, 1839).

Female : Chelicera with segment I, 102 μ ; II, 204 μ ; movable digit 87 μ, bidentate ; fixed digit tridentate ; pilus dentilis short, setiform (Text-fig. 50C). Four

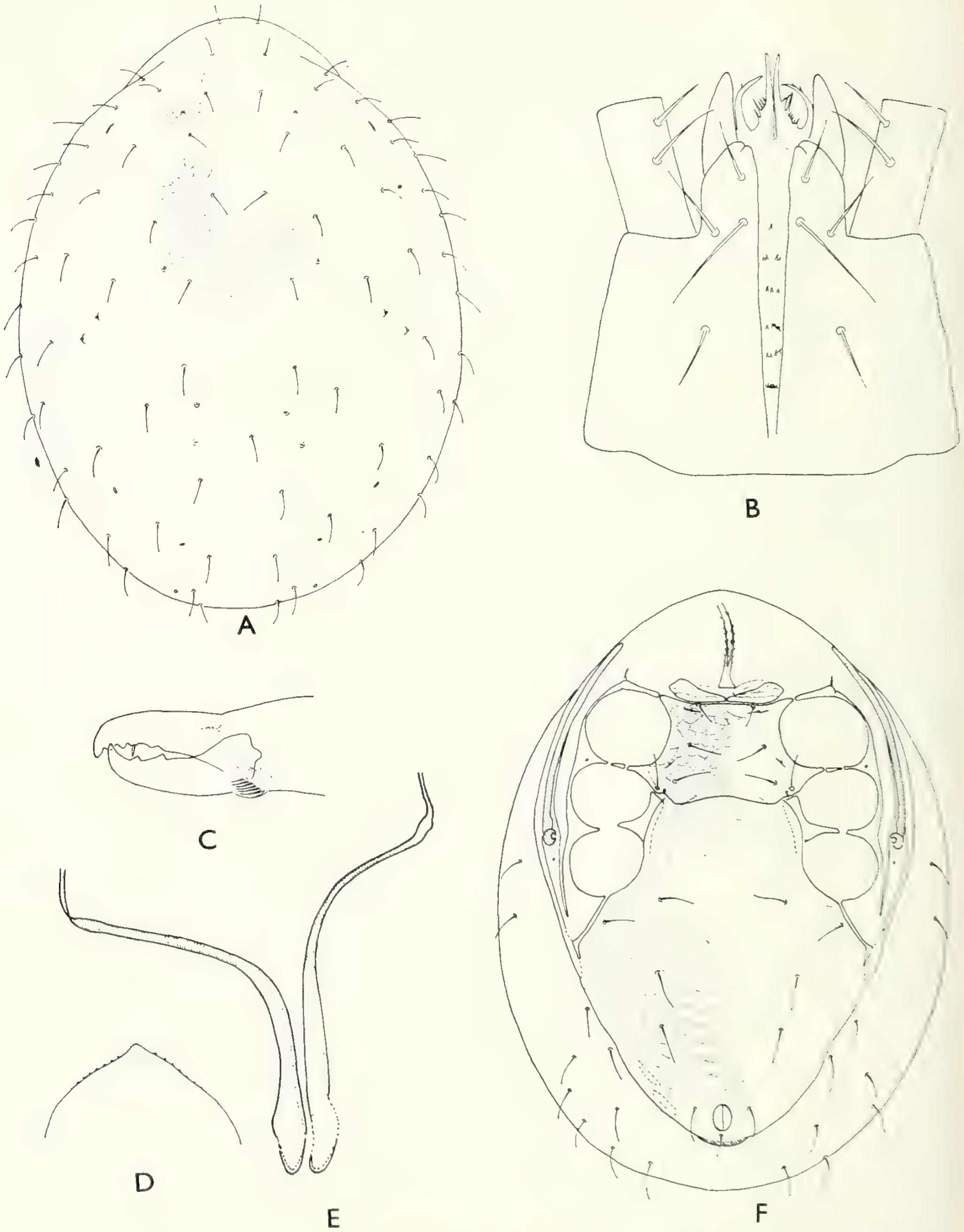


Fig. 50. *Ololaelaps sellnicki* Bregetova, female; dorsum of idiosoma (A); venter of gnathosoma (B); chelicera (C); tectum capituli (D); "spermathecal ducts" (E); venter of idiosoma (F).

pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 48 μ apart. Deutosternum with six transverse rows of denticles (1–5 per row); corniculi 60μ long; internal malae as in Text-fig. 50B. Tectum capituli with anterior margin very finely denticulate (Text-fig. 50D). Salivary styli conspicuous. Pedipalp (2–5–6–14) with three-tined apotele.

Dorsal shield (636 μ × 480 μ) with 37 pairs of simple, subequal setae distributed as in Text-fig. 50A, setae *z*1 and *z*3 being absent. A single accessory seta is present between the *J* series. Surface of shield granular with sculptured areas in the podonotal region.

Tritosternum with base 24 μ, laciniae 66 μ. Sterno-metasternal shield (102 μ × 132 μ) with four pairs of setae and three pairs of pores. Between *st*1, 60 μ; between *st*1 and *st*3, 87 μ. Genito-ventro-anal shield (264 μ × 264 μ) with four pairs of setae in the preanal region. Paranal setae 36 μ, postanal seta 21 μ. Chaetotaxy of opisthogaster as in Text-fig. 50F. Peritreme extends to middle of coxa I; anterior part of peritrematal shield fused with dorsal shield, posterior part fused with podal shield behind coxa IV and with genito-ventro-anal shield. Spermathecal ducts as in Text-fig. 50E.

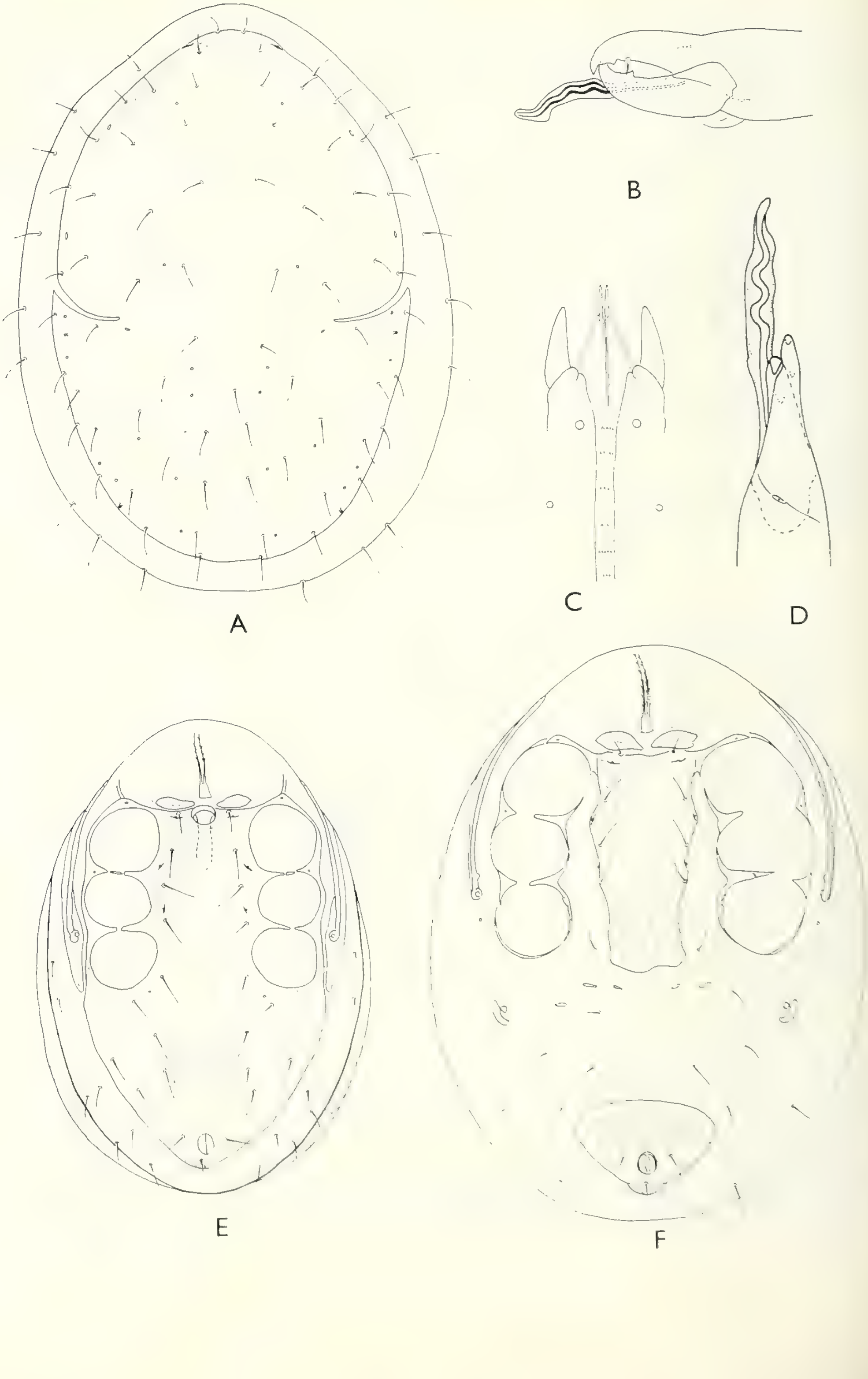
Legs with normal chaetotaxy. Tarsus II with ventral setae inflated basally, tapering to long, fine points. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	90/40	75/50	63/42	84/45
tibia	102/36	72/48	60/40	80/42
tarsus	168/32	126/40	114/36	156/36

Male: Chelicera with segment I, 60 μ; 282 μ; movable digit 63 μ (102 μ with spermadactyl), unidentate; groove of spermadactyl with sinous margins (Text-figs. 51 B and D); fixed digit unidentate, pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.*2 about 45 μ apart. Deutosternum with six transverse rows of denticles (2–5 per row); corniculi 48 μ long; internal malae fringed (Text-fig. 51C). Tectum, salivary styli and pedipalps as in female.

Dorsal shield (516 μ × 360 μ) with 37 pairs of setae and one unpaired accessory seta. Tritosternum with base 15 μ, laciniae 57 μ. Holoventral shield (408 μ × 93 μ) expanded behind coxae IV and fused with podal shields; with four pairs of setae and three pairs of pores in the sternal region, six pairs of setae in the genito-ventral region. Between *st*1, 54 μ; between *st*1 and *st*3, 87 μ. Paranal setae 27 μ, postanal seta 9 μ. Chaetotaxy of opisthogaster as in Text-fig. 51E. Peritreme extends to about middle of coxa I; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Legs with normal chaetotaxy. Tarsus II with seta pv_2 strongly inflated basally, terminating in a fine point. Length/width (in μ) of leg segments:


B
A
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	I	II	III	IV
genu	75/33	66/45	48/36	66/36
tibia	81/30	60/42	48/33	69/36
tarsus	144/27	108/36	99/30	132/30

Deutonymph : Chelicera with segment I, 72 μ ; II about 160 μ ; movable digit 66 μ. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 48 μ apart. Deutosternum with six transverse rows of denticles (3–6 per row) ; corniculi 40 μ long. Internal malae and pedipalps as in female.

Dorsal shield (624 μ × 396 μ) with lateral incisions, bearing 34 pairs of setae ; setae *z*1 and *z*3 absent ; setae *s*3, *s*6 and humeral seta on cuticle (Text-fig. 51A). Opisthonotal region with one accessory seta ; five pairs of *R* setae on the cuticle. Tritosternum with base 20 μ, laciniae 50 μ. Sternal shield (246 μ × 105 μ) with four pairs of setae and three pairs of pores. Between *st*1, 60 μ ; between *st*1 and *st*3, 102 μ. Anal shield (96 μ × 110 μ) with maximum width 162 μ ; paranal setae 27 μ ; postanal seta 18 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 51F. Peritreme extends to middle of coxa I ; anterior part of peritrematal shield free, extending a short distance beyond tip of peritreme ; posterior part not developed.

Legs with normal chaetotaxy. Tarsus II with setae *av* and *pv* stout basally, tapering to long, fine points. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	75/42	70/50	50/42	72/45
tibia	87/36	60/45	48/40	72/42
tarsus	150/33	93/40	105/33	144/40

HABITAT : Found in moss and decaying organic matter in Britain, Europe and Iceland.

NOTE : Bregetova & Koroleva (1964) have figured the dorsum of *O. sellnicki* with paravertical setae. Dr. Bregetova has kindly re-examined her specimens at our request and has confirmed that the paraverticals are actually absent as in our material.

Ololaelaps placentula (Berlese)

Laelaps placentula Berlese, 1887, *Acari, Myr. Scorp. Ital.* fasc. 44, no. 3.
Ololaelaps placentula: Sellnick, 1940, *Göteborgs Vetensk. Samh. Handl.* (5B), **6** (14): 69, fig. 49; Bregetova & Koroleva, 1964, *Parazit. Sb.* **22** : 70, figs.
Ololaelaps confinis Berlese, 1904, *Redia* **1** : 261.

Female : Chelicera with segment I, 90 μ ; II, 192 μ ; movable digit 102 μ, bidentate ; fixed digit with three teeth, two of which are very small and rounded ; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 66 μ apart,

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FIG. 51. *Ololaelaps sellnicki* Bregetova. A. Dorsum of idiosoma of deutonymph ; B. chelicera of male, internal view ; C. deutosternum and hypostome of male ; D. chelicera of male, dorsal view ; E. venter of idiosoma of male ; F. venter of idiosoma of deutonymph.

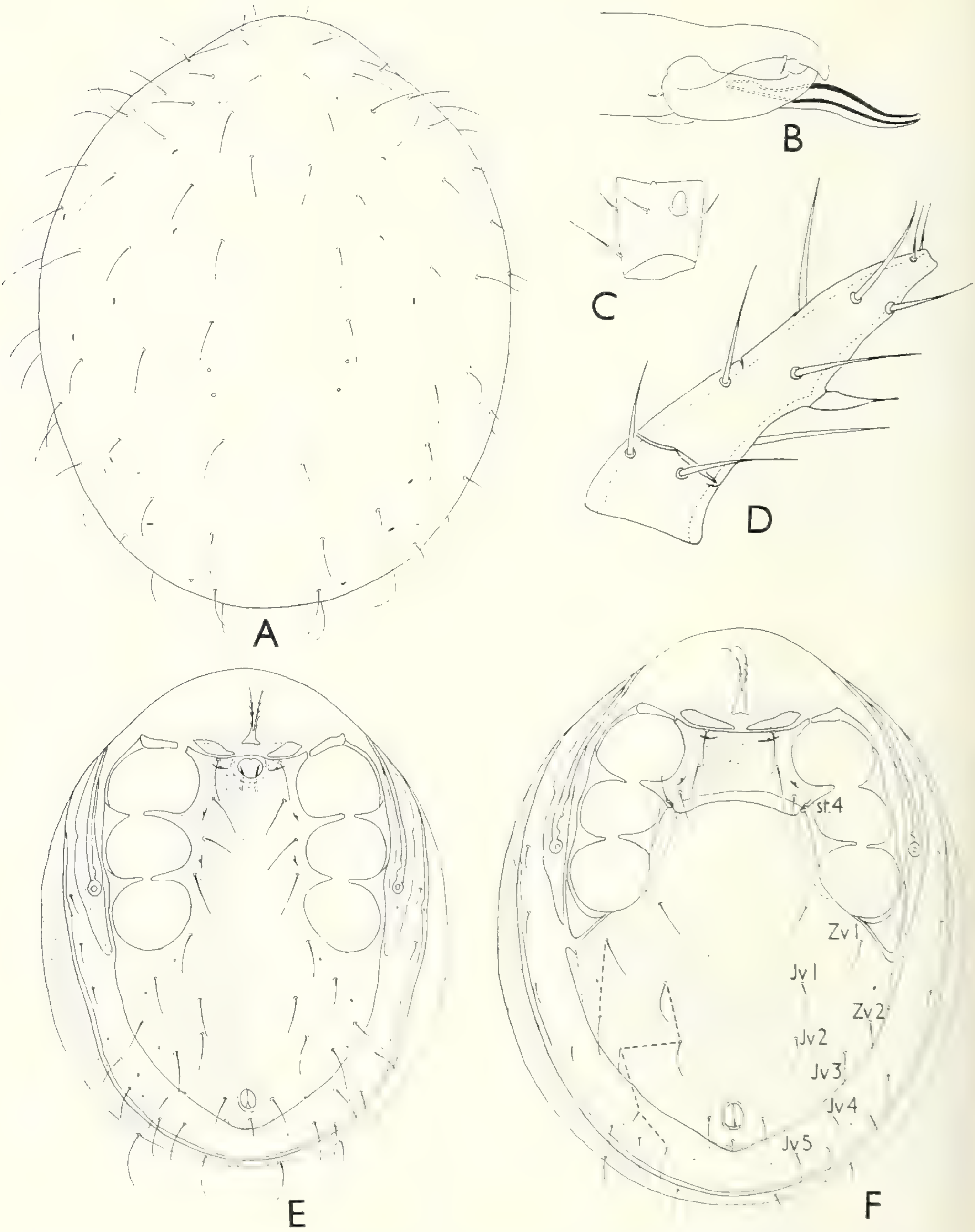

B
C
D
A
st.4
Zv1
Jv1
Zv2
Jv2
Jv3
Jv4
Jv5
E
F

Fig. 52. *Ololaelaps placentula* (Berlese). A. Dorsum of idiosoma of female; B. chelicera of male; C. genu III of male; D. tarsus II of male; E. venter of idiosoma of male; F. venter of idiosoma of female.

hyp.2 about 57 μ apart. Deutosternum with six transverse rows each of many denticles ; corniculi 63 μ ; internal malae and tectum captituli as in *I. sellnicki*. Salivary styli conspicuous, extending almost to tips of corniculi. Pedipalp (2–5–6–14) with three-tined apotele.

Dorsal shield (approximately 732 μ × 540 μ) with 39 pairs of simple setae distributed as in Text-fig. 52A ; Surface of shield granular, with faint reticulations ; no hypertrichy.

Tritosternum with base 27 μ, laciniae 84 μ. Sternal shield (80 μ × 132 μ) with four pairs of setae and three pairs of pores. Between *st*1, 80 μ ; between *st*1 and *st*3, 84 μ. Genito-ventro-anal shield (288 μ × 252 μ) expanded behind coxae IV, but not fused with podal or peritrematal shields ; with six pairs of setae in the preanal region. Paranal setae 36 μ, postanal seta 30 μ. Chaetotaxy of opisthogaster as in Text-fig. 52F. Peritreme extends to about middle of coxa I ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Legs with normal chaetotaxy ; tarsus II with ventral setae relatively stout basally, tapering to long, fine points. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	93/42	75/54	63/45	78/45
tibia	96/36	66/50	54/42	75/45
tarsus	165/33	126/42	120/38	160/38

Male : Chelicera with segment I, 75 μ ; II, 165 μ ; movable digit 75 μ (123 μ with spermadactyl), unidentate ; margins of spermadactyl groove smooth (Text-fig. 52B) ; fixed digit unidentate, pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp*.2 about 50 μ apart. Deutosternum with seven transverse rows each of many denticles ; corniculi 54 μ long ; hypostomal processes consist of a pair of slender, pilose triangles. Tectum capituli, salivary styli and pedipalps as in female.

Dorsal shield (570 μ × 460 μ) with 39 pairs of setae as in female. Tritosternum with base 21 μ, laciniae 63 μ. Holoventral shield (420 μ × 123 μ) expanded behind coxae IV, fused with podal but not with peritrematal shields ; with four pairs of setae and three pairs of pores in the sternal region, six pairs of setae in the genito-ventral region. Between *st*1, 70 μ ; between *st*1 and *st*3, 93 μ. Paranal setae 33 μ, postanal seta 24 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 52E. Peritreme extends beyond posterior margin of coxa I ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Legs with normal chaetotaxy. Genu III with seta *pv* reduced to a small " pimple " situated on a protuberance of the segment (Text-fig. 52C). Tarsus II with seta pv_2 inflated basally, tapering to a long, fine point (Text-fig. 52D). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	75/36	78/50	60/42	72/42
tibia	84/33	66/45	57/40	75/40
tarsus	150/30	132/35	117/34	144/38

Immature stages : The larva, protonymph and deutonymph of this species are described and figured by Bregetova & Koroleva (1964).

HABITAT : Found in moss and decaying organic matter in Britain, Europe and Iceland. Recorded from the nests of small mammals in the U.S.S.R.

Subfamily **HAEMOGAMASINAE** Oudemans

Haemogamasidae Oudemans, 1926, *Ent. Ber. Amst.* **7** (150) : 120.

Adults : Chelicerae chelate, dentate or edentate ; in dentate forms movable digit in the female bidentate, in the male unidentate. In some *Brevisterna* fixed digit in both sexes weakly sclerotized and transversely striated, movable digit of female with conspicuous hyaline lobe. Pilus dentilis simple or inflated ; dorsal seta conspicuous, rarely reduced to a microseta or absent ; fissures normal. Arthrodial processes present or absent, arthrodial membrane sometimes lobate (*Haemogamasus*). Spermadactyl grooved, relatively short, free distally but closely associated with the movable digit. Chaetotaxy of venter of gnathosoma normal. Pedipalps with five free segments, apotele two- or three-tined ; chaetotaxy normal (2–5–6–14). Palptrochanter rarely with weak medio-ventral ridge ; with sensory organ in *Eulaelaps*. Deutosternum with ten or more transverse rows of denticles ; denticles rarely in single file (*Brevisterna*). Corniculi horn-like, in the form of flattened lobes or membranous. Internal malae usually bipartite and conspicuous. Tectum capituli fimbriated and overhanging the hypostome, or weakly sclerotized with smooth margins (*Brevisterna*).

Dorsum of idiosoma in both sexes with entire shield or with abbreviated shield and a small setae-bearing pygidial shield in the female (*Brevisterna*). Primary chaetotaxy completely obliterated by secondary hypertrichy of both the dorsal shield and the unsclerotized cuticle. Dorsal setae simple or pilose.

Tritosternum normal, laciniae pilose ; lateral margins of basal region rarely denticulate (*Eulaelaps*). Sternal shield in the female normally with three pairs of setae and two pairs of pores, but with accessory setae in some species of *Haemogamasus* ; shield reduced and bearing only two pairs of setae and two pairs of pores in *Brevisterna*. Metasternal setae free. Genito-ventral shield usually with numerous setae. Anal shield normal or with accessory setae, opisthogastric cuticle showing hypertrichy. Metapodal shields large, subtriangular or subovate (*Eulaelaps*) or relatively small. Peritrematal shields free or fused with the podal shields posterior to coxae IV. Stigmata normal, peritremes well developed or reduced. Podal shields weakly developed. Male with holoventral shield, with or without accessory setae in the sternito-genital region, opisthogastric region densely setose ; or with sternito-genito-ventral and anal shields (*Ischyropoda*). Genital orifice presternal.

Segmental chaetotaxy of legs normal except for genu IV ($2—\frac{2}{1}, \frac{3}{0}—2$) in all species and rarely (*H. hirsutosimilis*) femur II ($2—\frac{5}{4}—1$) and femur III ($1—\frac{3}{2}—1$). Anterior spine on coxa II small or absent. Ambulacra with claws sometimes reduced on leg I. Femur II with one or more ventral setae hypertrophied in some males.

Larva and Protonymph : Insufficient data are available on these stages for their definition. Both stages have been described for *Haemogamasus ambulans* : Keegan, 1951, by Furman (1959). Hypertrichy of the idiosoma is apparent at the protonymphal stage in *Haemogamasus*.

Deutonymph : Gnathosoma with the general characteristcs of the female. Dorsal idiosomal sclerotization comprising a single shield with (*Eulaelaps* and *Haemogamasus*) or without (*Ischyropoda*) lateral incisions, or an abbreviated dorsal shield (podonotal) with mesonotal scutellae and fragments of the pygidial shield (*Brevisterna*). Dorsal chaetotaxy shows marked hypertrichy.

Tritosternum as in female. Sternito-genital shield with three pairs of sternal and one pair of metasternal setae, genital setae free, or with numerous accessory setae. Anal shield normal or with accessory setae ; opisthogastric cuticle showing hypertrichy. Podal shields usually small. Peritrematal shields free posteriorly ; stigmata and peritremes as in adult.

Leg chaetotaxy as in corresponding adult.

Key to the Genera of the British Haemogamasinae

1 Female with metapodal shields large, subtriangular, and flanking a broad genito-ventral shield ; palptrochanter with sensory organ (Text-fig. 62F) ; anterior rows of deutosternal denticles with 5 to 7 denticles per row in both sexes
EULAELAPS (p. 259)

– Female with metapodal shields small, sub-ovate ; genito-ventral shield relatively narrow ; palptrochanter lacking sensory organ ; anterior rows of deutosternal denticles with two to three denticles per row in both sexes
HAEMOGAMASUS (p. 239)

Genus ***HAEMOGAMASUS*** Berlese

Liponissus Kolenati, 1858, *Wien. ent. Monatschr.* **2** : 5.
Liponyssus Kolenati, 1859, *S.B. Akad. Wiss. Wien.* **35** : 172.
Haemogamasus Berlese, 1889, *Acar., Myr. Scorp. Ital.* fasc. 52, nos. 2 and 10.
Euhaemogamasus Ewing, 1933, *Proc. U.S. nat. Mus.* **82** (art. 30) : 3.
Groschaftella Samsinak, 1957, *Cslka. parasitol.* **4** : 270 (**syn. nov.**).

Type : *Haemogamasus hirsutus* Berlese, 1889.

Chelicerae chelate-dentate, rarely edentate ; pilus dentilis simple or inflated ; dorsal seta long, stout, rarely absent. Dorsal and anti-axial fissures conspicuous. Spermadactyl short, closely associated with the movable digit. Tectum fimbriated and overhanging the hypostome. Basis capituli with a pair of capitular setae ; hypostome with the normal three pairs of setae. Deutosternum with 10–18 transverse rows of denticles. Internal malae bipartite, conspicuous. Corniculi horn-like or in the form of flattened lobes. Salivary styli well developed. Pedipalps with normal chaetotaxy ; apotele two- or three-tined.

Dorsum of idiosoma with marked hypertrichy which completely obliterates the primary chaetotaxy. Dorsal shield entire in both sexes ; dorsal setae simple or pilose.

Tritosternum normal, pilose laciniae about three times the length of the base. Sternal shield in the female with the normal three pairs of setae and two or three pairs of pores ; with accessory setae in some species. Metasternal setae free. Genito-ventral shield flask-shaped with numerous setae. Anal shield pear-shaped, with the usual three setae associated with the anus, and with or without accessory setae. Opisthogastric integument densely setose. Metapodal shields small, peritrematal shield fused with expodal shield in the region of coxa IV. Male with holoventral shield, with or without accessory setae in the sternito-genital region ; opisthogastric region of shield densely setose.

Segmental chaetotaxy of legs normal except for genu IV $(2-\frac{2}{1}, \frac{3}{0}-2)$ and tibia IV $(2-\frac{2}{1}, \frac{2}{1}-2)$ in all species and femur II $(2-\frac{5}{4}-1)$ and femur III $(1-\frac{3}{2}-1)$ in *H. hirsutosimilis.*

The type of the genus *Liponyssus* Kolenati (*Liponyssus setosus* Kolenati, 1858) was so poorly described and figured that its identity has always been in doubt. In earlier standard works on the obligatory ectoparasitic "Laelaptidae" the genus was widely used to accommodate certain species now included in the Macronyssinae and Ewing (1923) proposed the subfamily Liponyssinae for *Liponyssus* sensu authors and certain related genera. Oudemans (1936) considered *L. setosus* to be " a totally different sort of mite " from the other species included in *Liponyssus* by authors, the majority of which were placed by him in *Macronyssus* for which he proposed the family Macronyssidae. Although certain authors have continued to use *Liponyssus* and Liponyssinae since Oudemans (1936) the general tendency has been for the suppression of *Liponyssus* sensu authors, especially since Fonseca's revisionary work in 1948.

A single damaged specimen, probably the type, of *Liponyssus setosus* Kolenati has recently been found in the Kolenati collection in Paris. This species is a male of *Haemogamasus horridus* Michael. The strict application of the Rules of Priority would necessitate the synonymizing of *Haemogamasus* Berlese with *Liponyssus* Kolenati. However this course would be contrary to the interests of nomenclatural stability especially since *Haemogamasus* and suprageneric taxa based upon it are so well established in the literature. We propose to submit an application to the International Commission on Zoological Nomenclature requesting its use of the plenary powers to suppress the genus *Liponyssus* Kolenati, 1858, its type species and the suprageneric categories based on the name *Liponyssus.*

KEY TO FEMALES

1 Sternal shield with the normal three pairs of setae only 2

– Sternal shield with accessory setae which are usually shorter than the primary sternal setae and vary in size, number and position on the shield 5

2 Posterior margin of the sternal shield deeply incised to a level midway between the first and second pairs of sternal setae (Text-fig. 60B). Anal shield usually with only the normal three setae. Dorsal and ventral surface of the idiosoma less densely setose than in the following species (Text-figs. 60A–B). **H. pontiger** (Berlese) (p. 257)

– Posterior margin of sternal shield at the most slightly concave (Text-fig. 59B). Anal shield with several accessory setae 3

3 First pair of sternal setae and hypostomal setae barbed. Dorsal shield, especially in the anterior and marginal regions, with many barbed setae. Tectum capituli narrow, pointed, with simple and multiple fimbriae. Pilus dentilis inflated (Text-fig. 59E). . . . . **H. nidi** Michael (p. 254)

– Sternal, hypostomal and dorsal setae smooth. Tectum capituli with gently rounded margin of simple and multiple fimbriae. Pilus dentilis short, setiform (Text-figs. 57A and C) 4

4 Postero-ventral margin of the idiosoma with at least one pair of setae conspicuously longer than the rest (Text-fig. 58B) ; sternal shield about as wide as long ; genito-ventral shield with 60 or more setae ; deutosternal denticles as in Text-fig. 58D. Associated with *Talpa* (Insectivora) . . . ***H. horridus*** Michael (p. 252)

– Postero-ventral margin of the idiosoma with setae subequal (Text-fig. 56B) ; sternal shield about $1\frac{1}{2}$ times wider than long ; genito-ventral shield with about 40–45 setae ; deutosternal denticles as in Text-fig. 56F. Associated with Muridae (Rodentia) . . . . ***H. arvicolarum*** (Berlese) (p. 250)

5 Femur II with 12 setae $(2—\frac{5}{4}—1)$, femur III with seven setae $(1—\frac{3}{2}—1)$. One pair of extremely long postero-ventral idiosomal setae about three times the length of the neighbouring setae (Text-fig. 55C) . ***H. hirsutosimilis*** Willmann (p. 246)

– Femur II with 11 setae $(2—\frac{5}{3}—1)$, femur III with six setae $(1—\frac{3}{1}—1)$. Without very long postero-ventral idiosomal setae ; longest pair at the most twice the length of the neighbouring setae 6

6 Chelae dentate ; palptrochanter with both setae pilose, not inflated. Genito-ventral shield with accessory setae restricted mainly to the posterior region. Many setae barbed(*st*1, *hyp*. 2–3, *c.s.*, many dorsal setae and most setae on the appendages). Dorsal setae uniform in size except at anterior and posterior margins. Anal shield wider than long . . . . . . ***H. ambulans*** (Thorell) (p. 244)

– Chelae edentate ; palptrochanter with inner seta inflated basally. Genito-ventral shield with accessory setae evenly distributed over entire surface. All setae smooth. Dorsal shield with large and small setae interspersed over its entire surface. Anal shield longer than wide . . . . . . ***H. hirsutus*** Berlese (p. 242)

Key to Males

1 Sternal region of holoventral shield with no accessory setae anterior to the level of the second pair of pores 2

– Holoventral shield with accessory setae distributed over the entire surface . . 5

2 First pair of sternal setae smooth (Text-fig. 58C). Tectum capituli with gently rounded margin of simple and multiple fimbriae. Chelicera with dorsal seta distinctly distal to base of fixed digit 3

– First pair of sternal setae barbed (Text-fig. 59C). Tectum captuli tapering, pointed, with fimbriate margin. Chelicera with dorsal seta proximal to base of fixed digit 4

3 Femur II with av_1 short, spinose, conspicuously different from other ventral setae (Text-fig. 56E). Postero-ventral idiosomal setae subequal (Text-fig. 56D). Spermdactyl without retrose spur (Text-fig. 57D) . ***H. arvicolarum*** Berlese (p. 251)

– Femur II with av_1 setiform, similar to other ventral setae. At least one pair of postero-ventral idiosomal setae conspicuously longer than the neighbouring setae (Text-fig. 58C). Spermadactyl with a stout retrose spur (Text-fig. 57B). ***H. horridus*** Michael (p. 254)

4 Ventral seta on femur III setiform. Holoventral shield with dense covering of setae (Text-fig. 59C). Peritrematal shields fused posteriorly with holoventral shield and with podal elements of coxa IV. Pilus dentilis inflated (Text-fig. 59F) ***H. nidi*** (Michael (p. 255)

– Ventral seta on femur III short, spinose. Holoventral shield with relatively sparse covering of setae (Text-fig. 60D). Peritrematal shields free posteriorly. Pilus dentilis slender, setiform (Text-fig. 60E) . . ***H. pontiger*** (Berlese) (p. 259)

5 First pair of sternal setae barbed . . . . ***H. ambulans*** (Thorell)

– All sternal setae smooth 6

6 Femur II with 12 setae (4 ventrals, of which two are blunt and peg-like). A pair of very long setae near posterior end of idiosoma about three times the length of the neighbouring setae. Setae on dorsal shield subequal in size, except at anterior and posterior margins. Fixed digit of chelicera relatively short and broad, with a short, antero-median projection (Text-fig. 55E). ***H. hirsutosimilis*** Willmann (p. 248)

– Femur II with 11 setae (three ventrals, all stout, pointed, spine-like). No very long setae near posterior end of body, longest seta at the most 1½ times the length of the neighbouring setae. Dorsal shield with large and small setae interspersed over its entire surface. Fixed digit of chelicera relatively long, slender, hook-like, with a prominent median expansion (Text-fig. 53E) . . ***H. hirsutus*** Berlese (p. 244)

Haemogamasus hirsutus Berlese

Haemogamasus hirsutus Berlese, 1889, *Acari, Myr. Scorp. Ital.* fasc. 52, no. 2.
Keegan, 1951, *Proc. U.S. nat. Mus.* **101** : 210, fig. 42.
Bregetova, 1956, *Opred. Faune SSSR.* **61** : 140, figs. 290–293, 322–325.

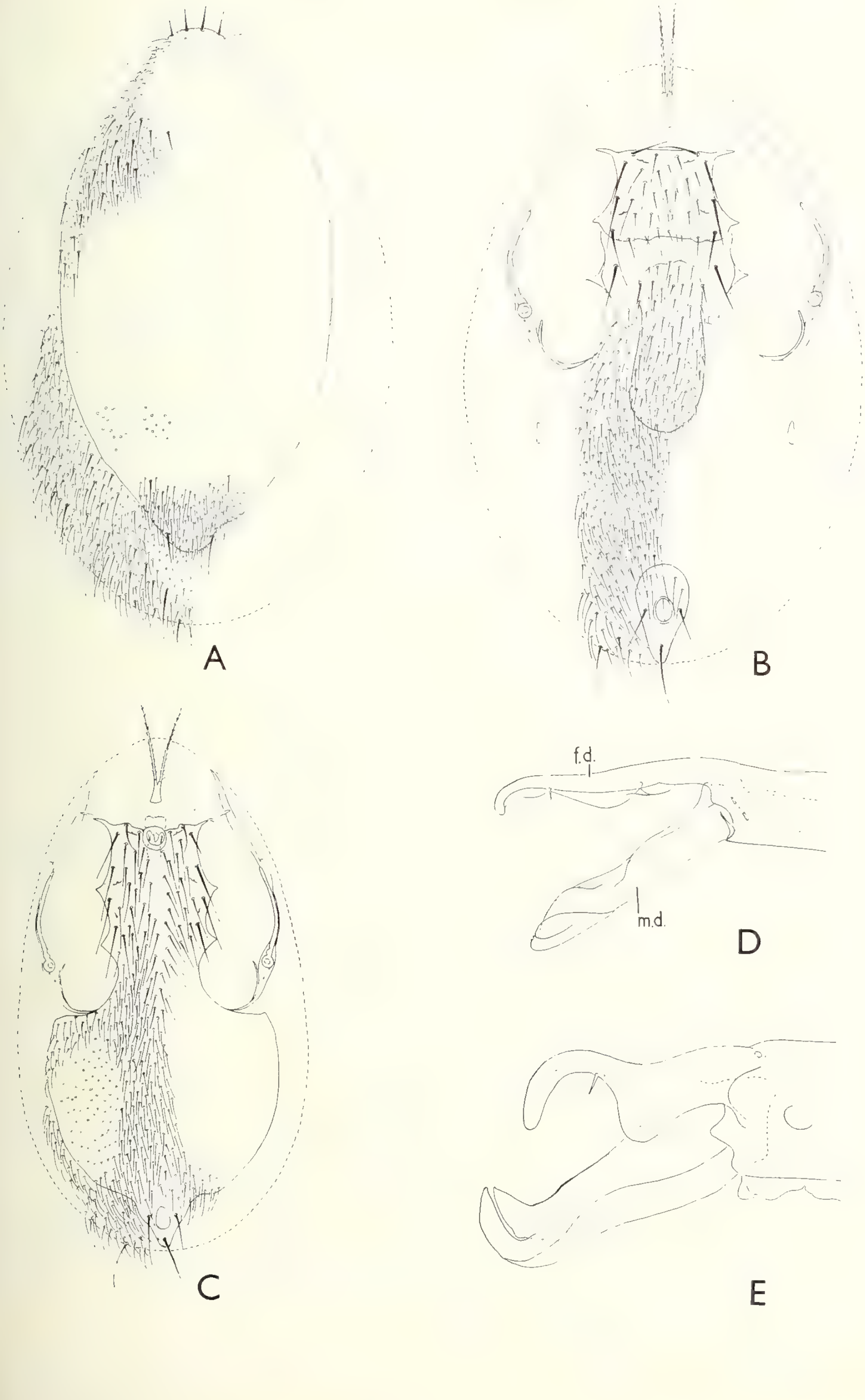
Female : Chelicera with segment I, 144 μ ; II, 300 ; movable digit 87 μ ; both digits edentate ; pilus dentilis short, setiform (Text-fig. 53D), dorsal seta apparently absent. Four pairs of gnathosomal setae with *c.s.* about 120 μ apart ; *hyp*.2 about 84 μ apart. Deutosternum with 14 transverse rows of denticles ; corniculi membranous, about 63 μ long ; internal malae with inner processes slender, pilose, outer processes fimbriate (Evans & Till, 1965, Text-fig. 4C). Tectum capituli narrow, with anterior margin fimbriate. Salivary styli conspicuous, tubular, curved. Pedipalp (2–5–6–14) with three-tined apotele, one being very small ; palptrochanter with inner seta inflated basally.

Dorsal shield (1,164 μ × 636 μ) densely covered with simple setae of variable length (Text-fig. 53A). Surface of shield granular with some weakly defined reticulations.

Tritosternum with base 60 μ, laciniae 228 μ ; presternal area reticulate, with minute spines. Sternal shield (174 μ × 234 μ) with the usual three pairs of sternal setae and about 25 accessories ; with three pairs of pores, the pair usually associated with the metasternal setae being on the posterior margin of the shield ; metasternal setae free. Between *st*1, 150 μ ; between *st*1 and *st*3, 180 μ. Genito-ventral shield relatively slender with numerous accessory setae distributed over entire shield. Anal shield (168 μ × 96 μ) with the usual three setae and five accessories ; paranal setae 123 μ, postanal seta 108 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 53B. Peritreme extends to posterior margin of coxa II ; peritrematal shield free anteriorly, fused posteriorly with podal shield of coxa IV.

Chaetotaxy of legs differs from normal pattern in that genu IV has two posterolateral setae and tibia IV has the dorsal setal pattern (2–2) instead of (1–3). All the

FIG. 53. *Haemogamasus hirsutus* Berlese. A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. venter of idiosoma of male ; D. chelicera of female ; E. chelicera of male.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leg setae are smooth. Distal margins of most leg segments denticulate ventrally. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	222/60	156/100	150/78	204/72
tibia	228/54	156/90	162/66	222/60
tarsus	330/48	264/66	342/54	498/54

Male : Chelicera with segment I, 114 μ ; II, 222 μ ; movable digit 78 μ (87 μ with spermadactyl) ; both digits edentate (Text-fig. 53E) ; pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 99 μ apart ; *hyp.*2 about 72 μ apart. Deutosternum with 13 transverse rows of denticles ; corniculi 54 μ long. Tectum capituli with anterior and lateral margins fimbriate. Internal malae, salivary styli and pedipalps as in female.

Dorsal shield (1,026 $\mu \times 520$ μ) as in female. Tritosternum with base 50 μ, laciniae 165 μ. Holoventral shield (840 $\mu \times 198$ μ) with the usual sternal, metasternal and anal setae recognizable ; accessory setae present over entire surface of shield (Text-fig. 53C). Par- and postanal setae subequal, about 96 μ long. Peritremes and peritrematal shields as in female.

Chaetotaxy of legs as in female ; relatively stouter setae on femur II (ventrals), genu and tibia II (*av*) and tarsus II (*mv* and av_2). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	198/54	132/84	114/66	180/60
tibia	204/48	138/78	144/60	204/60
tarsus	264/42	186/54	264/48	414/48

HABITAT : Found in Britain in the nest and on the body of *Talpa europaea* Linn. and on the field vole *Microtus agrestis* (Linn.). Also recorded from a variety of rodents in the U.S.S.R. and Europe.

Haemogamasus ambulans (Thorell)

Dermanyssus ambulans Thorell, 1872, *Öfv. Vet.-Akad. Forh.* **2** : 164.
Hypoaspis ambulans: Trägårdh, 1904, *Fauna Arctica* **4** : 33, figs.
Haemogamasus ambulans: Bregetova, 1953, *Parazit. Sb.* **15** : 316 ; and 1956, *Opred. Faune SSSR.* **61** : 147, figs.
Haemogamasus alaskensis Ewing, 1925, *Proc. biol. Soc. Wash.* **38** : 138.
Keegan, 1951, *Proc. U.S. nat. Mus.* **101** : 213, fig. 43.
Haemogamasus avisugus Vitzthum, 1930, *Zool. Jahrb.* **60** : 397.
Haemogamasus sternalis Ewing, 1933, *Proc. U.S. nat. Mus.* **82** : 3, pl. 1, fig. 2.
Haemogamasus pavlovskyi Bregetova, 1949, *Parazit. Sb.* **11** : 179, figs.

Female : Chelicera with segment I, 105 μ ; II, 160 μ ; movable digit 54 μ, bidentate ; fixed digit tridentate ; pilus dentilis setiform ; dorsal seta long and

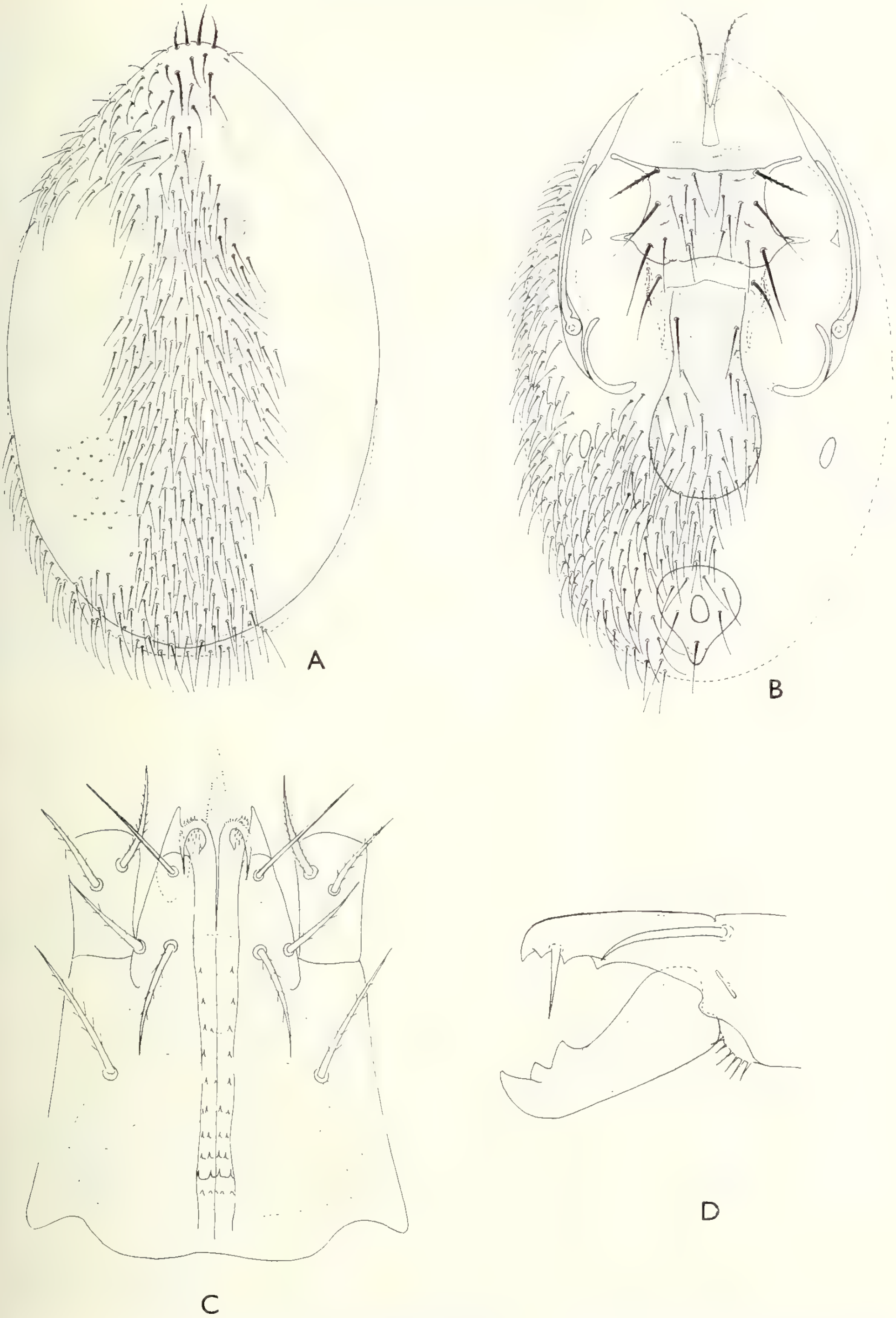

FIG. 54. *Haemogamasus ambulans* (Thorell), female; dorsum of idiosoma (A); venter of idiosoma (B); venter of gnathosoma (C); chelicera (D).

stout (Text-fig. 54D). Four pairs of gnathosomal setae with *c.s.* about 105 μ apart, *hyp.*2 about 75 μ apart ; *hyp.*2–3 and *c.s.* barbed. Deutosternum with ten transverse rows of denticles (2–5 per row) ; corniculi 40 μ long ; internal malae as in Text-fig. 54C. Tectum capituli narrow, pointed, fimbriate (Evans & Till, 1965 ; Text-fig. 3C). Salivary styli conspicuous, extending beyond tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele ; both trochantal setae barbed.

Dorsal shield (1,008 μ × 612 μ) densely covered with setae mostly of uniform length (Text-fig. 54A) ; some anterior and marginal setae barbed. Surface of shield granular, reticulations most distinct in opisthonotal area.

Tritosternum with base 57 μ, laciniae 150 μ. Sternal shield (132 μ × 190 μ) with the usual three pairs of sternal setae and about 14 accessories, and with three pairs of pores ; metasternal setae free. Between *st*1, 150 μ ; between *st*1 and *st*3, 120 μ ; *st*1 barbed. Genito-ventral shield (276 μ × 120 μ) with a pair of genital setae and about 36 accessories distributed chiefly on the posterior part of the shield. Anal shield (123 μ × 130 μ) with the usual three anal setae and four or five accessories ; paranal setae 68 μ ; postanal seta 78 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 54B. Peritreme extends to anterior third of coxa II ; peritrematal shield free anteriorly, fused posteriorly with podal shields of coxa IV.

Chaetotaxy of legs differs from normal pattern in that genu IV bears two postero-lateral setae and tibia IV bears two antero- and two postero-dorsal setae. All leg setae barbed except terminal setae on tarsi (ad_1, pd_1, av_1, pv_1, al_1, pl_1, pv_2 on tarsi II–IV, as well as av_2 on tarsi III–IV, and *mv* on tarsus IV). Distal margins of all segments except tarsi serrated. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	156/54	120/60	114/54	168/50
tibia	168/48	120/57	120/48	180/48
tarsus	228/42	210/45	264/42	372/42

HABITAT : Found in the nest of *Riparia riparia* (Linn.) in Gloucestershire, Britain. Recorded in the literature from the nests of birds, from insectivores, bats, sables, and a variety of rodents in Germany, the U.S.S.R., Greenland, Spitsbergen and North America.

Haemogamasus hirsutosimilis Willmann

Haemogamasus hirsutosimilis Willmann, 1952, *Z. Parasitenk.* **15** : 403, figs.
Bregetova, 1956, *Opred. Faune SSSR.* **61** : 141, figs.

Female : Chelicera with segment I, 84 μ ; II, 156 μ ; movable digit 60 μ, bidentate ; fixed digit with two large and two very small teeth ; pilus dentilis short, setiform, dorsal seta long (Text-fig. 55B), Four pairs of simple gnathosomal setae with

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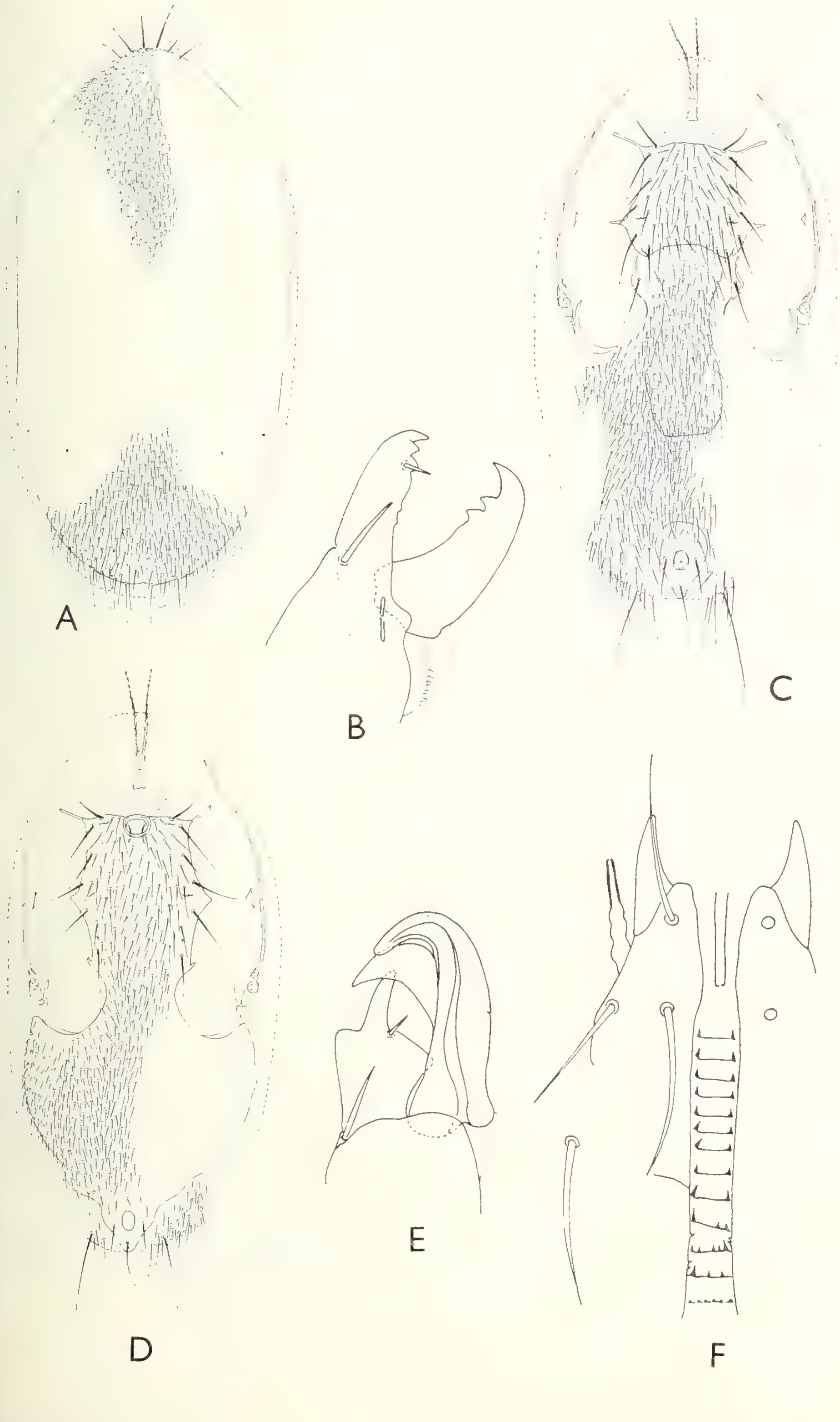
FIG. 55. *Haemogamasus hirsutosimilis* Willmann. A. Dorsum of idiosoma of female ; B. chelicera of female ; C. venter of idiosoma of female ; D. venter of idiosoma of male ; E. chelicera of male ; F. deutosternum and hypostome of female.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c.s. about 96 μ apart, *hyp.*2 about 70 μ apart. Deutosternum with 13 transverse rows of denticles (2–6 per row) as in Text-fig. 55F. Corniculi 40 μ long ; internal malae with long, pointed inner and short, broad, outer lobes, all pilose. Tectum capituli slender, pointed, deeply denticulate. Salivary styli conspicuous. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (1,032 μ × 564 μ) with a dense covering of setae mostly of subequal length, those on the posterior margin being considerably longer ; vertical setae long and stout, not barbed (Text-fig. 55A). Surface of shield granular.

Tritosternum with base barbed, 50 μ long ; laciniae 150 μ. Sternal shield (186 μ × 216 μ) with the usual sternal setae, numerous accessories, and three pairs of pores ; metasternal setae free. Between *st*1, 60 μ ; between *st*1 and *st*3, 174 μ. Genitoventral shield with numerous setae distributed over its entire surface. Anal shield (126 μ × 90 μ) with the usual three anal setae and five accessories ; paranal setae 110 μ ; postanal seta 117 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 55C ; a pair of extremely long setae at the posterior end of the body. Peritreme extends nearly to posterior margin of coxa I ; peritrematal shield free anteriorly, fused posteriorly with podal shield of coxa IV ; pore on posterior shield situated at tip of small tubercle.

Chaetotaxy of legs differs from the normal pattern in that femur II bears 12 setae (4 ventrals), femur III bears 7 setae (2 ventrals), genu IV bears two postero-lateral setae and tibia IV has two antero- and two postero-dorsal setae ; all leg setae simple. Coxae all with rows of denticles on ventral surface ; distal margins of all segments except tarsi serrated. Ambulacrum IV nearly one-and-a-half times as long as the others. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	174/54	120/72	108/66	156/60
tibia	180/45	120/63	120/60	168/54
tarsus	240/42	192/50	237/48	318/42

Male : Chelicera with segment I, 60 μ ; II, 150 μ ; fixed digit short and broad with an anterior projection ; movable digit and spermadactyl strongly curved (Text-fig. 55E). Four pairs of gnathosomal setae with *c.s.* about 85 μ apart, *hyp.*2 about 63 μ apart. Corniculi 42 μ long ; other gnathosomal features as in female.

Dorsal shield (780 μ × 438 μ) as in female. Tritosternum with base 33 μ, laciniae 105 μ ; presternal area as in female. Holoventral shield 648 μ long, with a dense covering of accessory setae (Text-fig. 55D) ; true sternal setae difficult to distinguish. Par- and postanal setae subequal, about 75 μ long. Peritreme extends to anterior margin of coxa II ; anterior tip of peritrematal shield terminates very close to dorsal

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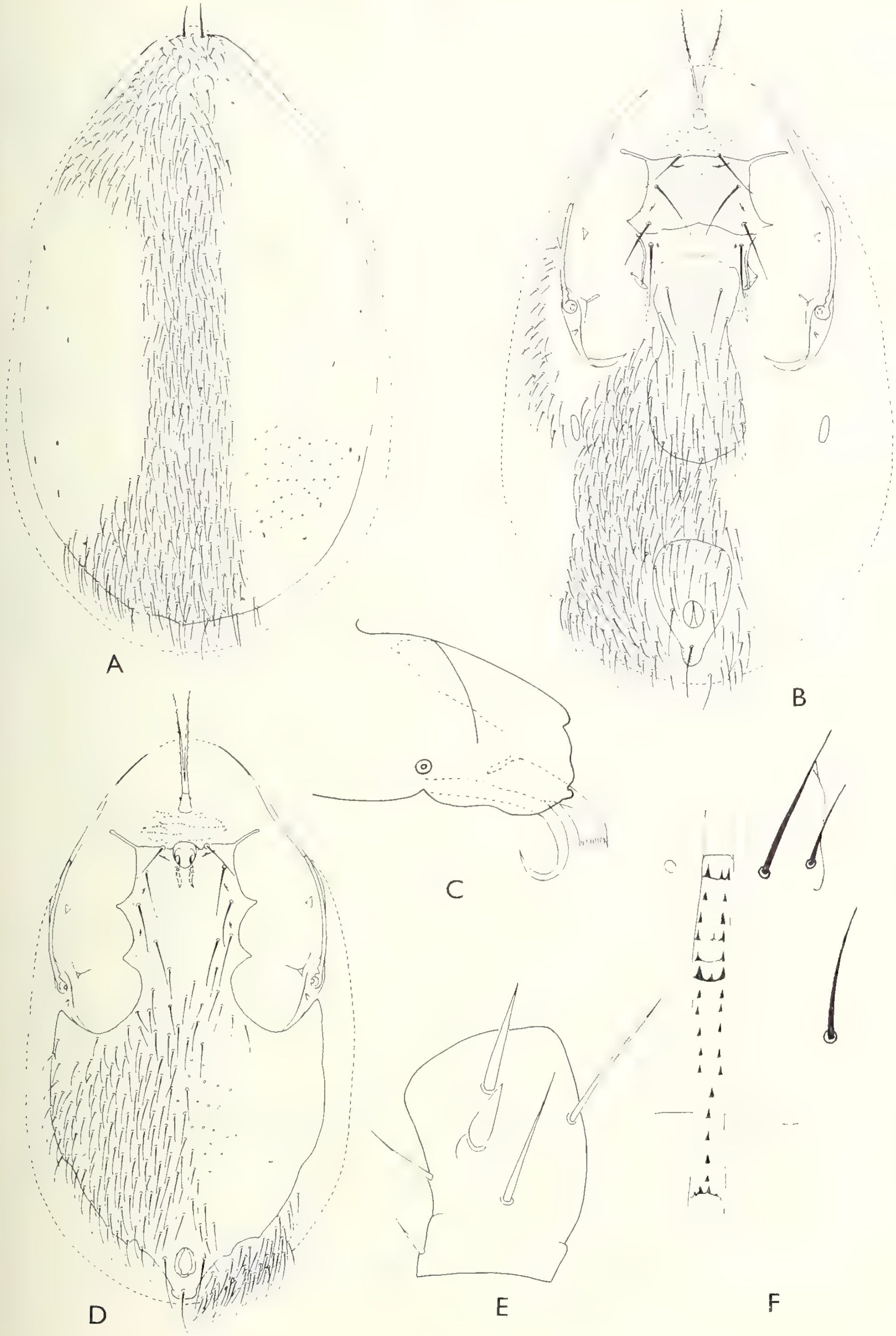
FIG. 56. *Haemogamasus arvicolarum* Berlese. A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. corniculus of female, lateral view ; D. venter of idiosoma of male ; E. femur II of male ; F. deutosternum of female.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shield but appears to end freely ; posterior part of shield fused with podal elements of coxa IV.

Chaetotaxy and ornamentation of legs as in female. Stout, blunt, peg-like setae are present on femur II (pv_{2-3}), genu II (*av*), tibia II (*av*) and tarsus II (*mv*) ; seta av_2 on tarsus II is very stout but pointed. Seta pd_2 on tarsus IV is extremely long, about two-thirds the length of the tarsus. Ambulacrum IV relatively shorter than in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	160/48	102/66	96/50	138/54
tibia	156/42	105/57	108/50	150/50
tarsus	207/40	156/42	204/40	270/40

HABITAT : Found in a mole's nest in Gloucestershire, Britain. Recorded from moles, voles and field mice in Europe and the U.S.S.R.

Haemogamasus arvicolarum Berlese

Haemogamasus horridus var. *arvicolarum* Berlese, 1920, *Redia* **14** : 166.
Haemogamasus arvicolarum: Turk, 1945, *Ann. Mag. nat. Hist.* (2) **12** : 785, figs.

Female : Chelicera with segment I, 120 μ ; II, 270 μ ; movable digit 80 μ, bidentate ; fixed digit bidentate with terminal hook ; pilus dentilis short, setiform ; dorsal seta long, stout, blunt (Text-fig. 57C). Four pairs of simple gnathosomal setae with *c.s.* about 123 μ apart, *hyp.2* about 93 μ apart. Deutosternum with 17 transverse rows of denticles (1–4 per row) ; corniculi broad, weakly sclerotized (Text-fig. 56C and F) ; internal malae as in *H. horridus*. Tectum capituli with a rounded anterior margin provided with numerous simple or multiple fimbriae. Salivary styli conspicuous, reaching nearly to tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele ; inner trochantal seta barbed.

Dorsal shield (1,320 μ × 840 μ) with a dense covering of subequal setae (Text-fig. 56A). Setae *j1* considerably stouter than the others but not barbed ; a few marginal setae have a minute barb near the tip. Surface of shield granular with sculpturing anteriorly and reticulations posteriorly.

Tritosternum with base 63 μ, laciniae 258 μ ; a small spine on each side of the base. Presternal area with small spines on the reticulations. Sternal shield (156 μ × 240 μ) with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between *st1*, 90 μ ; between *st1* and *st3*, 168 μ. Genital shield with about 44 setae distributed mainly on the posterior part. Anal shield (258 μ × 138 μ) with maximum width 186 μ, bearing the usual three anal setae and about 13 accessories ; paranal setae 114 μ ; postanal seta 126 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 56B ; some marginal setae barbed. Peritreme extends to posterior margin of coxa II ; peritrematal shield fused anteriorly with dorsal shield and posteriorly with podal shield of coxa IV.

Chaetotaxy of legs differs from normal pattern in that genu IV has two postero-lateral setae and tibia IV has two antero- and two postero-dorsal setae. All leg setae simple. Coxae bear rows of small denticles; distal margins of all segments except tarsi serrated ventrally. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	207/72	168/102	150/84	192/78
tibia	222/66	168/90	168/72	240/72
tarsus	306/60	240/66	330/66	456/66

Male: Chelicera with segment I, 84 μ; II, 200 μ; movable digit with spermadactyl, 150 μ; pilus dentilis short, setiform; dorsal seta as in female, but situated a considerable distance distal to the base of the fixed digit (Text-fig. 57D). Four pairs of simple gnathosomal setae with *c.s.* about 105 μ apart; *hyp.2* about 93 μ apart. Deutosternum with 14 transverse rows of denticles (1–3 per row); corniculi 57 μ long; internal malae, tectum and pedipalps as in female.

Dorsal shield (1,092 μ × 600 μ) as in female. Tritosternum with spine on each side of base; with base 60 μ, laciniae 210 μ. Presternal area with small spines on the reticulations. Holoventral shield (876 μ × 192 μ) with the usual sternal and metasternal setae and three pairs of pores in the sternal region, and the usual three anal setae. Numerous accessory setae are distributed on the genito-ventral region

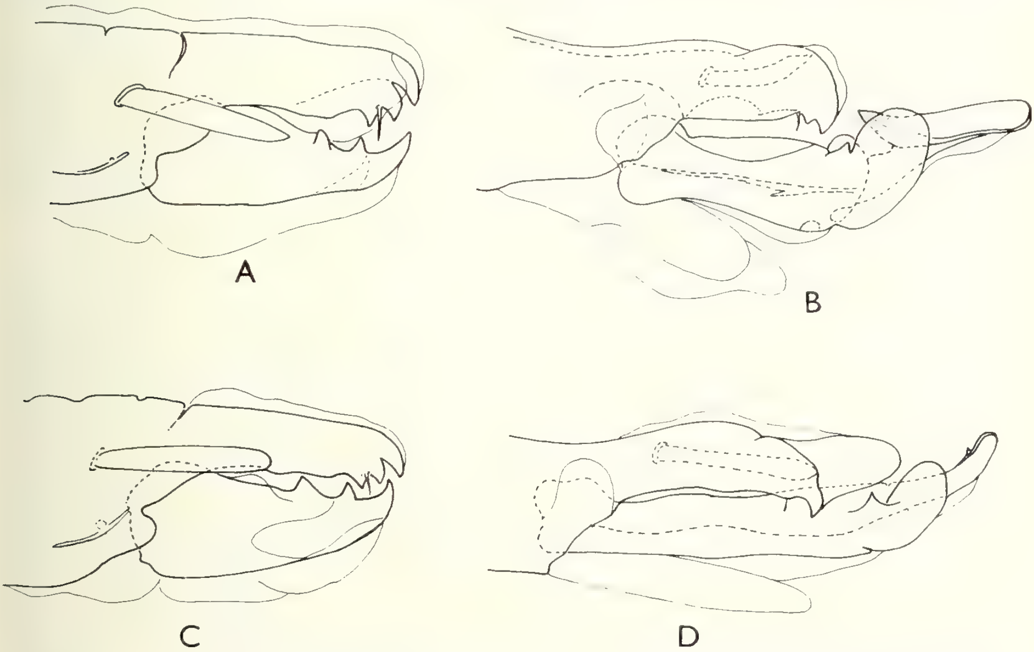


FIG. 57. A–B. *Haemogamasus horridus* Michael; chelicera of female (A) and male (B). C–D. *Haemogamasus arvicolarum* Berlese; chelicera of female (C) and male (D).

and may extend to the level of the metasternals (Text-fig. 56D). Between *st*1, 87 μ ; between *st*1 and *st*3, 123 μ. Paranal setae 90 μ ; postanal seta 80 μ. Peritreme extends approximately to posterior border of coxa II ; peritrematal shield fused anteriorly with dorsal shield, posteriorly with podal shield of coxa IV.

Chaetotaxy of legs as in female. Femur II with seta av_1 short and stout (Text-fig. 56E). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	186/66	150/87	144/72	180/66
tibia	198/54	144/78	156/60	204/66
tarsus	270/54	192/60	264/54	384/54

HABITAT : Found on moles, voles and field mice and in their nests in Britain and Europe.

Haemogamasus horridus Michael

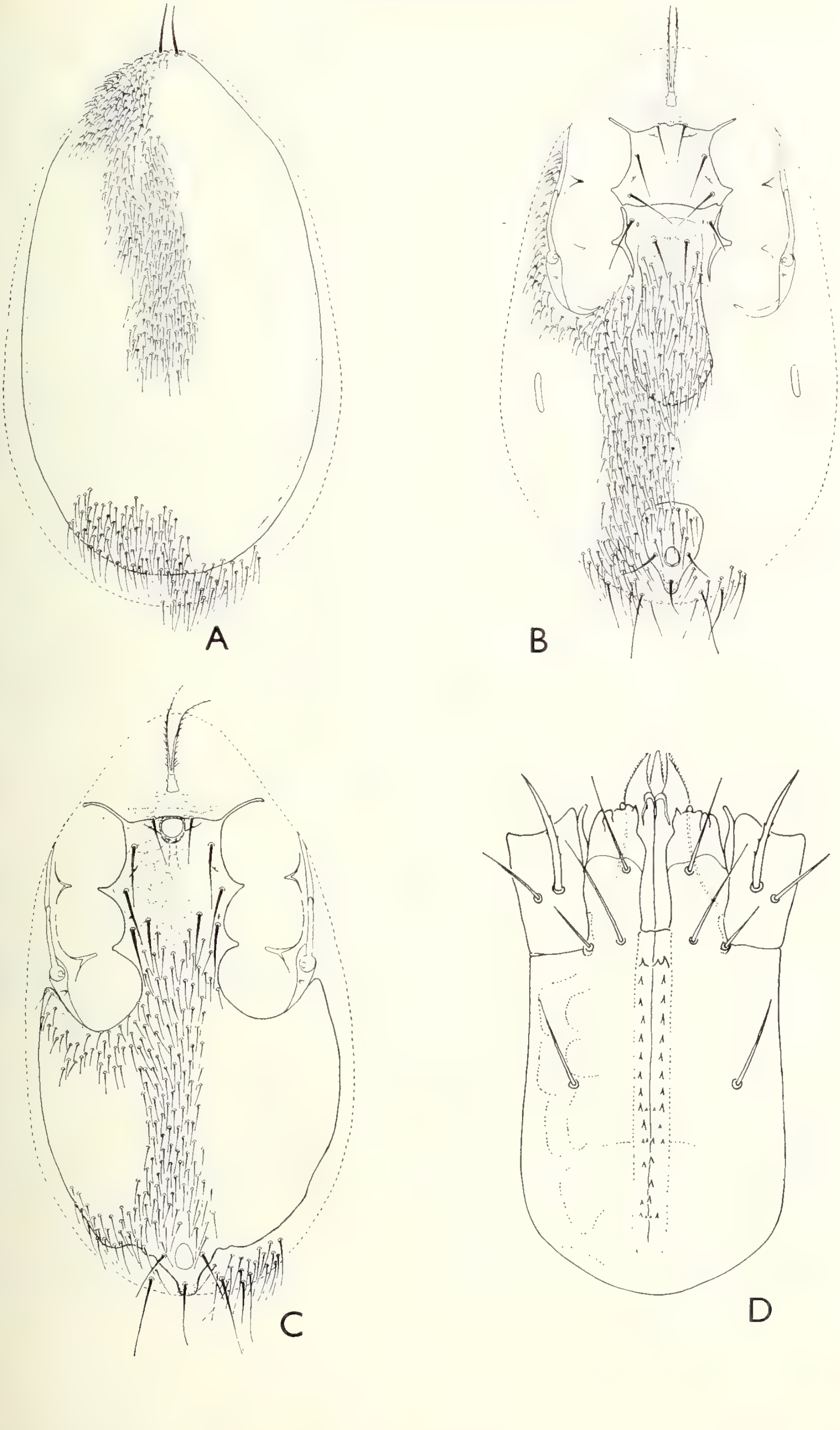
Haemogamasus horridus Michael, 1892. *Trans. Linn. Soc. Lond.* **5** : 312, figs.
Bregetova, 1956, *Opred. Faune SSSR.* **61** : 131, figs.

Female : Chelicera with segment I, 96 μ ; II, 222 μ ; movable digit 75 μ, bidentate ; fixed digit bidentate, with terminal hook ; pilus dentilis short, setiform ; dorsal seta long and stout (Text-fig. 57A). Four pairs of simple gnathosomal setae with *c.s.* about 126 μ apart ; *hyp.*2 about 100 μ apart. Deutosternum with 15 transverse rows of denticles (1–5 denticles per row) ; corniculi broad, membranous, about 45 μ long ; internal malae fringed, comprising slender inner and broad, triangular, outer processes (Text-fig. 58D). Tectum capituli has a rounded anterior margin provided with numerous simple or multiple fimbriae. Salivary styli conspicuous. Pedipalp (2–5–6–14) with two-tined apotele ; inner trochantal seta barbed.

Dorsal shield (1,536 μ × 864 μ) with a dense covering of setae for the most part subequal in length, but tending to become longer towards the posterior margin ; vertical setae long and stout (Text-fig. 58A). Surface of shield granular and reticulate.

Tritosternum with base 60 μ, laciniae 276 μ ; a small spine present on each side of the base. Presternal area with small spines on the reticulations. Sternal shield (234 μ × 240 μ) with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between *st*1, 80 μ ; between *st*1 and *st*3, 222 μ. Genitoventral shield with about 70 setae. Anal shield (234 μ × 138 μ ; maximum width 180 μ) with the usual three anal setae and about 14 accessories. Paranal setae 132 μ, postanal seta 150 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 58B ; at least one pair of setae at posterior margin considerably longer than the

FIG. 58. *Haemogamasus horridus* Michael. A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. venter of idiosoma of male ; D. venter of gnathosoma of female.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neighbouring setae ; some setae with fine, sparse barbs. Peritreme extends to anterior margin of coxa III ; anterior tip of peritrematal shield fused with dorsal shield at level of *j*1 ; posterior part fused with podal shields behind coxae IV.

Chaetotaxy of legs normal except genu IV ($2—\frac{2}{1}, \frac{3}{0}—2$) and tibia IV ($2—\frac{2}{1}, \frac{2}{1}—2$). Leg setae apparently simple ; distal margins of most leg segments serrated ventrally. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	252/75	192/108	168/90	222/90
tibia	276/66	192/98	186/90	264/90
tarsus	348/54	288/72	372/72	504/70

Male : Chelicera with segment I, 102 μ ; II, 168 μ ; spermadactyl with a stout retrose spur (Text-fig. 57B). Four pairs of simple gnathosomal setae with *c.s.* about 102 μ apart, *hyp.*2 about 84 μ apart. Deutosternum with 15 transverse rows of denticles (2–3 per row). Corniculi 54 μ long ; other gnathosomal features as in female.

Dorsal shield (1,212 $\mu \times 600 \mu$) as in female. Tritosternum with base 48 μ, laciniae 210 μ. Holoventral shield (984 $\mu \times 204 \mu$) with the usual four pairs of sternal and metasternal setae, and also bearing numerous accessory setae which extend anteriorly to the level of *st*4. Between *st*1, 80 μ ; between *st*1 and *st*3, 168 μ. Paranal setae 110 μ, postanal seta 135 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 58C. Peritreme extends to anterior margin of coxa III ; peritrematal shield fused at its anterior tip with the dorsal shield, and posteriorly with the holoventral shield.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	222/66	156/90	150/75	192/78
tibia	240/57	162/84	168/75	234/78
tarsus	300/54	258/63	330/63	450/60

HABITAT : Associated with moles (*Talpa europaea* Linn.) in Britain, Europe and the U.S.S.R.

Haemogamasus nidi Michael

Haemogamasus nidi Michael, 1892, *Trans. Linn. Soc. Lond.* **5** : 314, figs.
Bregetova, 1956, *Opred. Faune SSSR.* **61** : 134, figs.
Haemogamasus michaeli Oudemans, 1903, *Tijdschr. ned. dierk. Ver.* (2) **8** : 87.
Eulaelaps ambulans (Thorell) Trägårdh, 1910, *Nat. Unter. Sarekgebirges Swed. Lap.* **4** (4) : 435, figs. 116–122.

Female : Chelicera with segment I, 90 μ ; II, 147 μ ; movable digit 48 μ, bidentate ; fixed digit bidentate ; pilus dentilis inflated basally; dorsal seta long and stout (Text-fig. 59E). Four pairs of barbed gnathosomal setae with *c.s.* about 93 μ apart, *hyp.2* about 70 μ apart. Deutosternum with ten transverse rows of denticles (2–5 per row); corniculi 30 μ long; internal malae with long, pointed inner and short, broad, outer processes, all pilose. Salivary styli conspicuous, extending beyond tips of corniculi. Tectum capituli slender, pointed, fimbriate. Pedipalp (2–5–6–14) with two-tined apotele. Palptrochanter with both setae barbed.

Dorsal shield (984 μ × 576 μ) with a dense covering of subequal setae (Text-fig. 59A); those on posterior margin slightly longer; setae *j*1 longer, stouter and barbed. Many marginal and anterior setae barbed. Surface of shield granular.

Tritosternum with base 48 μ, laciniae 150 μ. Sternal shield (108 μ × 168 μ) with three pairs of setae and three pairs of pores; metasternal setae free. Between *st*1, 120 μ; between *st*1 and *st*3, 120 μ; *st*1 barbed. Genito-ventral shield bears numerous setae distributed mostly on posterior two-thirds of shield. Anal shield (110 μ × 105 μ) with five or six accessories in addition to the usual three anal setae; paranal setae 66 μ; postanal seta 84 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 59B. Peritreme extends to middle of coxa II; anterior tip of peritrematal shield free, but lying very close to dorsal shield; posterior part fused with podal shield of coxa IV.

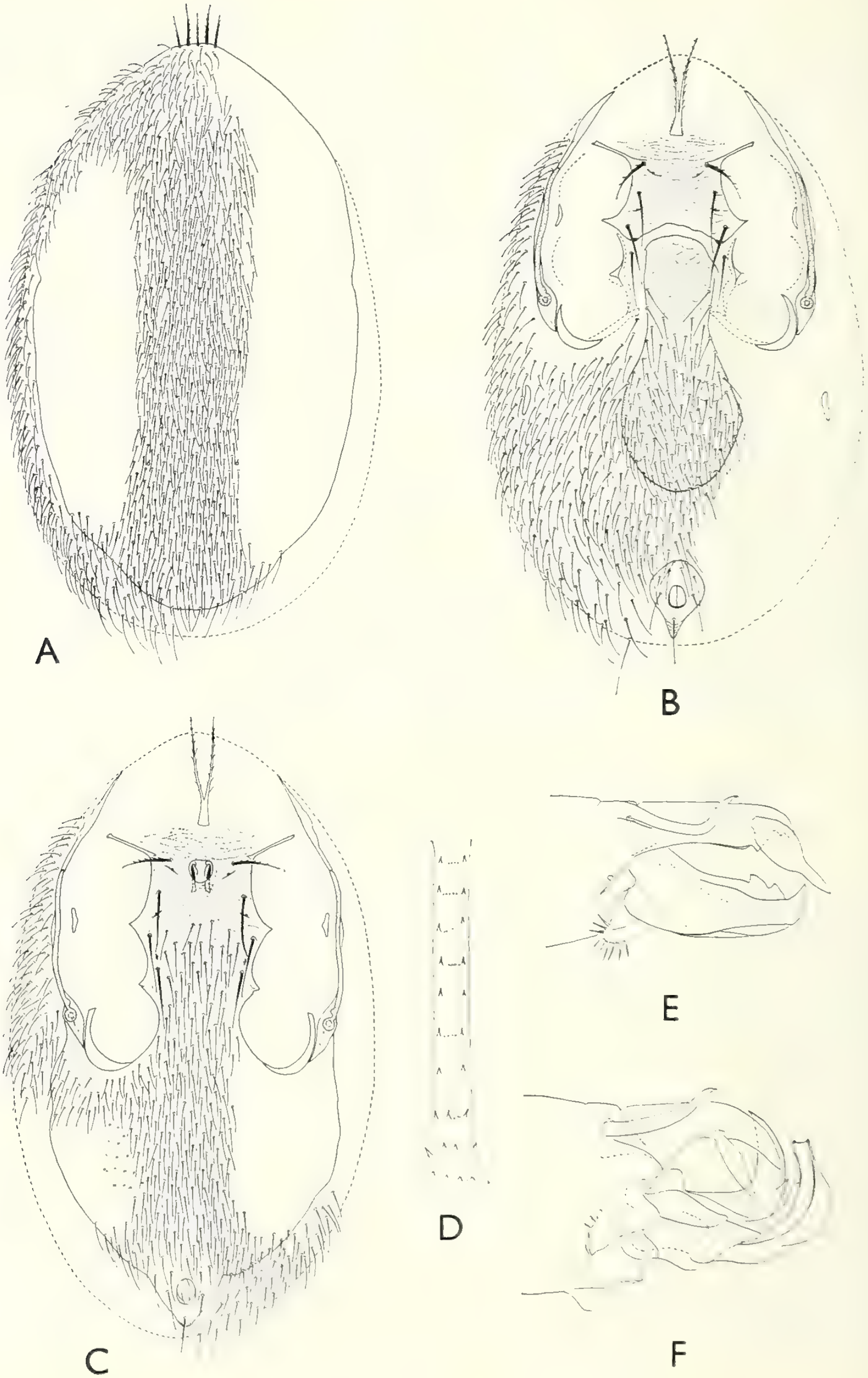
Chaetotaxy of legs differs from normal pattern in that genu IV has two posterolateral setae and tibia IV has two antero- and two postero-dorsal setae; setae ad_1 and pd_1 are not visible on tarsi II–IV. Most leg setae barbed. Distal margins of all segments except tarsi serrated. Ambulacrum IV nearly one-and-a-half times as long as ambulacrum III. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	144/54	114/72	90/60	138/57
tibia	156/48	108/66	102/48	150/48
tarsus	216/42	168/48	216/42	315/42

Male: Chelicera with segment I, 75 μ; II, 140 μ. Cheliceral digits and spermadactyl as in Text-fig. 59F. Four pairs of gnathosomal setae with *c.s.* about 84 μ apart, *hyp.2* about 66 μ apart. Deutosternum with ten transverse rows of denticles (2–7 per row). Internal malae, salivary styli, tectum and pedipalps as in female.

Dorsal shield (840 μ × 480 μ) as in female. Tritosternum with base 40 μ, laciniae 120 μ, presternal area as in female. Holoventral shield (624 μ × 150 μ) with the usual sternal and metasternal setae, and with numerous accessory setae distributed over almost entire shield and extending anteriorly to between *st*2 and *st*3 (Text-fig. 59C). Between *st*1, 90 μ; between *st*1 and *st*3, 110 μ; *st*1 barbed. Par- and postanal setae subequal, about 60 μ long. Peritreme extends to middle of coxa II; anterior tip of peritrematal shield fused with dorsal shield, posterior tip fused with podal shield of coxa IV.

Chaetotaxy and ornamentation of legs as in female. Stout setae present on femur II (*av*), genu II (*av*), tibia II (*av*) and tarsus II (av_2 and *mv*). Length/width (in μ) of leg segments:


A
B
C
D
E
F

	I	II	III	IV
genu	132/48	108/66	96/48	132/48
tibia	138/42	108/60	96/48	144/45
tarsus	192/36	144/42	186/36	282/36

HABITAT: Found in Britain, Europe and the U.S.S.R. chiefly on the bodies and in the nests of a variety of rodents. Also recorded from insectivores, small carnivores and birds.

Haemogamasus pontiger (Berlese)

Laelaps (*Eulaelaps*) *pontiger* Berlese, 1904, *Redia* **1** : 260.
Bregetova, 1956, *Opred. Faune SSSR.* **61** : 129, figs.
Groschaftella pontiger: Samsinak, 1957, *Cslka. parasitol.* **4** : 270, figs. 1–2.
Haemogamasus oudemansi Hirst, 1914, *Bull. ent. Res.* **5** : 122, pls. 14–16.
Keegan, 1951, *Proc. U.S. nat. Mus.* **101** : 240, figs. 48–49.
Eulaelaps mawsoni Womersley, 1937, *Austral. Antarctic Exped.* 1911–1914 : *Scientific Rep. ser. C. Zool. & Bot.* **10** : 19, pl. 12, figs. 4–7.

Female: Chelicera with segment I, 102 μ; II, 162 μ; movable digit 63 μ, bidentate; fixed digit bidentate, pilus dentilis setiform, dorsal seta long and stout (Text-fig. 60C). Four pairs of gnathosomal setae with *c.s.* about 87 μ apart, *hyp.*2 about 66μ apart; *hyp.*1 simple, *hyp.*2–3 and *c.s.* barbed. Deutosternum with 14 transverse rows of denticles (2–6 per row); corniculi 50 μ long; internal malae as in male (Text-fig. 60G). Tectum capituli slender, pointed, fimbriate. Salivary styli conspicuous. Pedipalp (2–5–6–14) with three-tined apotele (Text-fig. 60F); both trochantal setae barbed.

Dorsal shield (840 μ × 495 μ) with numerous setae distributed as in Text-fig. 60A. Setae *j*1 considerably stouter than the others, with fine barbs; some of the other anterior and antero-lateral setae also barbed. Surface of shield granular, with sculpturing on the podonotal and reticulations on the opisthonotal part.

Tritosternum with base serrated, 50 μ long; laciniae 126 μ. Presternal area with small spines on the reticulations. Sternal shield (42 μ × 160 μ) deeply concave posteriorly, with three pairs of setae and three pairs of pores; metasternal setae free. Between *st*1, 117 μ; between *st*1 and *st*3, 123 μ; *st*1 barbed. Genito-ventral shield (300 μ × 114 μ) enlarged posteriorly, with maximum width 246 μ; bearing a pair of genital setae and about 16 accessories on the posterior part of the shield. Anal shield (99 μ × 111 μ) with two small anterior protuberances; paranal setae 60 μ; postanal seta 78 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 60B. Peritreme extends a little beyond posterior border of coxa II; peritrematal shield free anteriorly, fused posteriorly with podal shield of coxa IV; pore in posterior part with thickened rim.

FIG. 59. *Haemogamasus nidi* Michael. A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. venter of idiosoma of male; D. deutosternum of female; E. chelicera of female; F. chelicera of male.

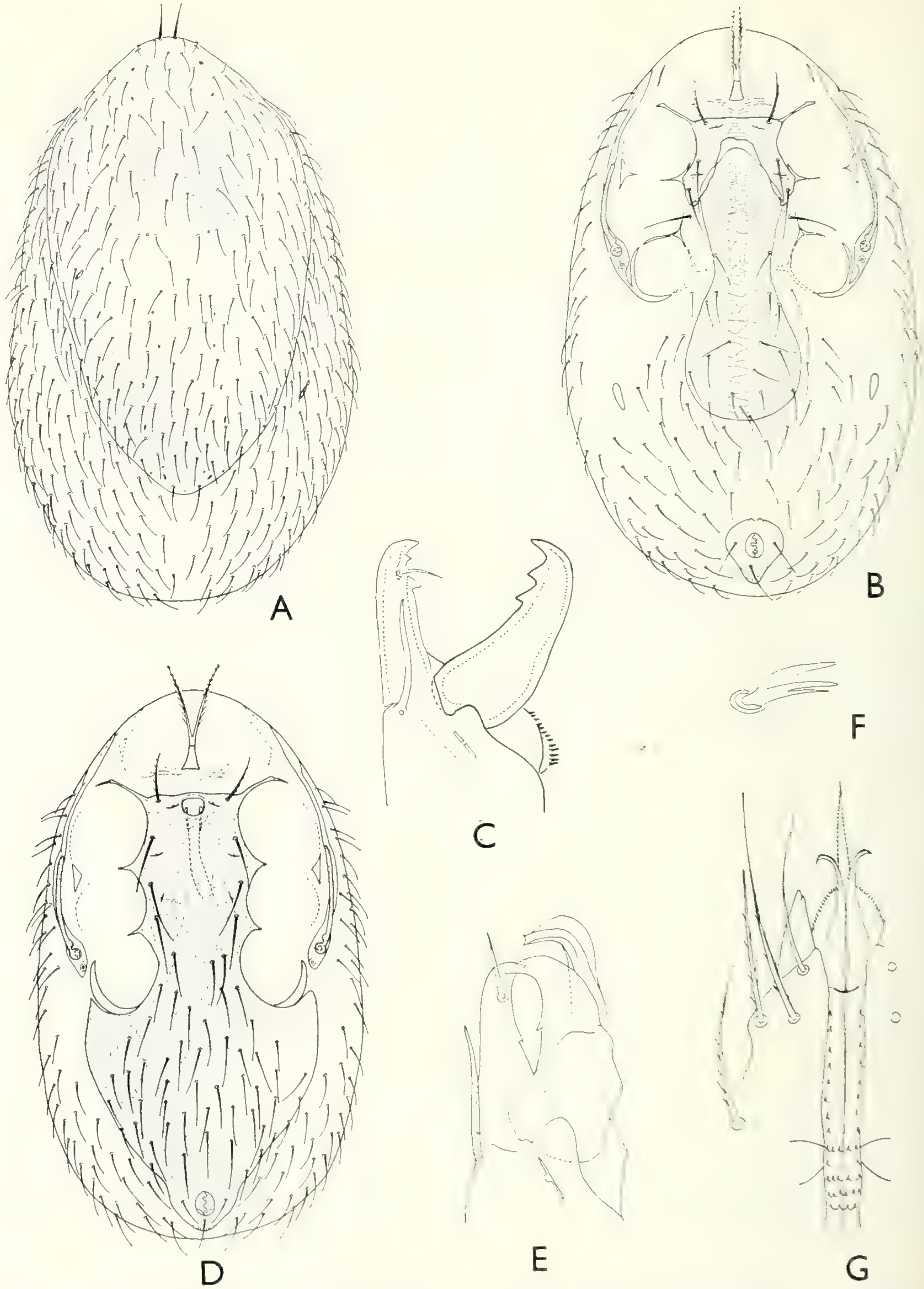


FIG. 60. *Haemogamasus pontiger* (Berlese). A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. chelicera of female ; D. venter of idiosoma of male ; E. chelicera of male ; F. apotele of pedipalp ; G. venter of deutosternum and hypostome of male.

Chaetotaxy of legs differs from normal pattern in that genu IV has two postero-lateral setae and tibia IV has two antero- and two postero-dorsal setae. Setae ad_1 and pd_1 at the extremities of tarsi II–IV are extremely minute and inconspicuous. Tarsus IV with seta pd_2 very long, three-fifths the length of the tarsus. Most leg setae barbed except terminal ones on tarsi. Distal margins of some segments faintly serrated. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	150/45	108/57	90/50	138/48
tibia	162/40	117/54	105/45	150/42
tarsus	246/36	192/40	210/36	300/36

Male : Chelicera with segment I, 70 μ ; II, 126 μ ; movable digit unidentate, 45 μ long (54 μ with spermadactyl) ; fixed digit unidentate ; dorsal seta long and stout ; pilus dentilis setiform (Text-fig. 60E). Four pairs of gnathosomal setae as in female with *c.s.* about 72 μ apart, *hyp.2* about 54 μ apart. Deutosternum with 13 transverse rows of denticles ; corniculi 45 μ long ; internal malae as in Text-fig. 60G. Tectum capituli, salivary styli and pedipalps as in female.

Dorsal shield (660 μ × 384 μ) as in female. Tritosternum with base 40 μ, laciniae 102 μ. Presternal area as in female. Holoventral shield (552 μ × 126 μ) with four pairs of setae and three pairs of pores in the sternal region, numerous setae distributed over the genito-ventral region (Text-fig. 60D). Between *st1*, 90 μ ; between *st1* and *st3*, 110 μ ; *st1* barbed. Paranal setae 36 μ ; postanal seta 48 μ. Peritreme extends a little beyond posterior margin of coxa II ; peritrematal shield free anteriorly and posteriorly, although anterior tip lies very close to dorsal shield.

Chaetotaxy of legs as in female ; short, stout, blade-like setae on femur III (*v*) and genu III (*pv*). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	130/40	102/51	90/44	126/42
tibia	138/36	102/48	100/40	138/40
tarsus	222/36	156/36	180/33	270/33

HABITAT : A cosmopolitan, facultative parasite recorded from rodents, a mole (*Talpa europaea* Linn.) and a bat ; also free-living in a variety of habitats including barley, sugar, wheat and rice straw, rice hulls and flax tow.

Genus *EULAELAPS* Berlese

Eulaelaps Berlese, 1903, *Zool. Anz.* **27** : 13.
Hemilaelaps Hull, 1918, *Trans. nat. Hist. Soc. Northumb.* **4** : 61 (*lapsus* for *Eulaelaps*).
Rhinolaelaps Fonseca, 1960, *Acarologia* **2** : 17.

Type : *Gamasus stabularis* Koch, 1836.

Medium to strongly sclerotized mites up to 1,000 μ in length. Chelicerae chelate-dentate, movable digit bidentate in the female, unidentate in the male. Pilus dentilis relatively long and simple. Dorsal seta and fissures normal. Spermadactyl short, grooved. Arthrodial processes present at base of movable digit in the female. Capitular and hypostomal setae normal. Deutosternum with ten or more transverse rows of denticles, four to seven denticles per row. Corniculi horn-like, internal malae elongate, fringed. Pedipalpal chaetotaxy normal, apotele two-tined. Palp-trochanter with unique sensory organ ventrally. Tectum capituli with anterior and lateral margins deeply denticulate.

Dorsum of idiosoma densely hypertrichous except for region of dorsal hexagon (*j*5, *z*5, *j*6) in some species. Dorsal setae simple or minutely pilose.

Tritosternum normal with lateral margins of basal region denticulate. No distinct pre-endopodal shields. Sternal shield in the female with three pairs of setae and two pairs of pores. Genito-ventral shield large with numerous setae. Anal shield free with normal three setae. Opisthogastric integument hypertrichous. Metapodal shields in the female very large and usually sub-triangular in outline. Peritrematal shields free in the female. Male with holoventral shield; peritrematal shields free or fused with the shield. Podal shields weakly developed posterior to coxae IV.

Segmental chaetotaxy of legs normal except genu IV ($2-\frac{2}{1}, \frac{3}{0}-2$). Coxa II with a small anterior spine. Ambulacra with claws sometimes strongly reduced on leg I.

Key to Females

1 Genito-ventral shield of female with lateral incisions posterior to the genital setae, lateral margins angular, bearing 47–52 opisthogastric setae; no setae on cuticle between genito-ventral and anal shields (Text-fig. 61F). Tarsus II with some spine-like setae (Text-fig. 61C) . . . . . **E. stabularis** Koch (p. 260)

– Genito-ventral shield without lateral incisions, lateral margins rounded, bearing about 26 opisthogastric setae; setae present on cuticle between genito-ventral and anal shield (Text-fig. 62A). Tarsus II with some stout, spur-like setae (Text-fig. 62E) **E. novus** Vitzthum (p. 263)

Key to Males

1 Tarsus II with setiform and spiniform setae; femur II without sclerotized protuberance ventrally . . . . **E. stabularis** Koch (p. 262)

– Tarsus II with setiform and stout, spur-like setae; femur II with conspicuous protuberance ventrally distal to fissure . . . . **E. novus** Vitzthum (p. 265)

Eulaelaps stabularis (Koch)[6]

Gamasus stabularis Koch, 1836, *Deutschl. C.M.A.* fasc. 27, no. 1.
Eulaelaps stabularis: Vitzthum, 1927, *Jen. Z. Naturwiss.* **62** : 162.
Bregetova, 1956, *Opred. Faune SSSR.* **61** : 100, figs.
Laelaps oribatoides Michael, 1892, *Trans. Linn. Soc. Lond. Zool.* **5** : 315, figs.
Eulaelaps arcualis (Koch) Trägårdh, 1912, *Arch. zool. exp. gen.* **48** : 577, figs. 90–93.
Eulaelaps oudemansi Turk, 1945, *Parasitology* **36** : 137.

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[6] According to Johnston (1959) *Laelaps pedalis* Banks, 1909 and *L. propheticus* Banks, 1909 are also synonyms of *E. stabularis*.

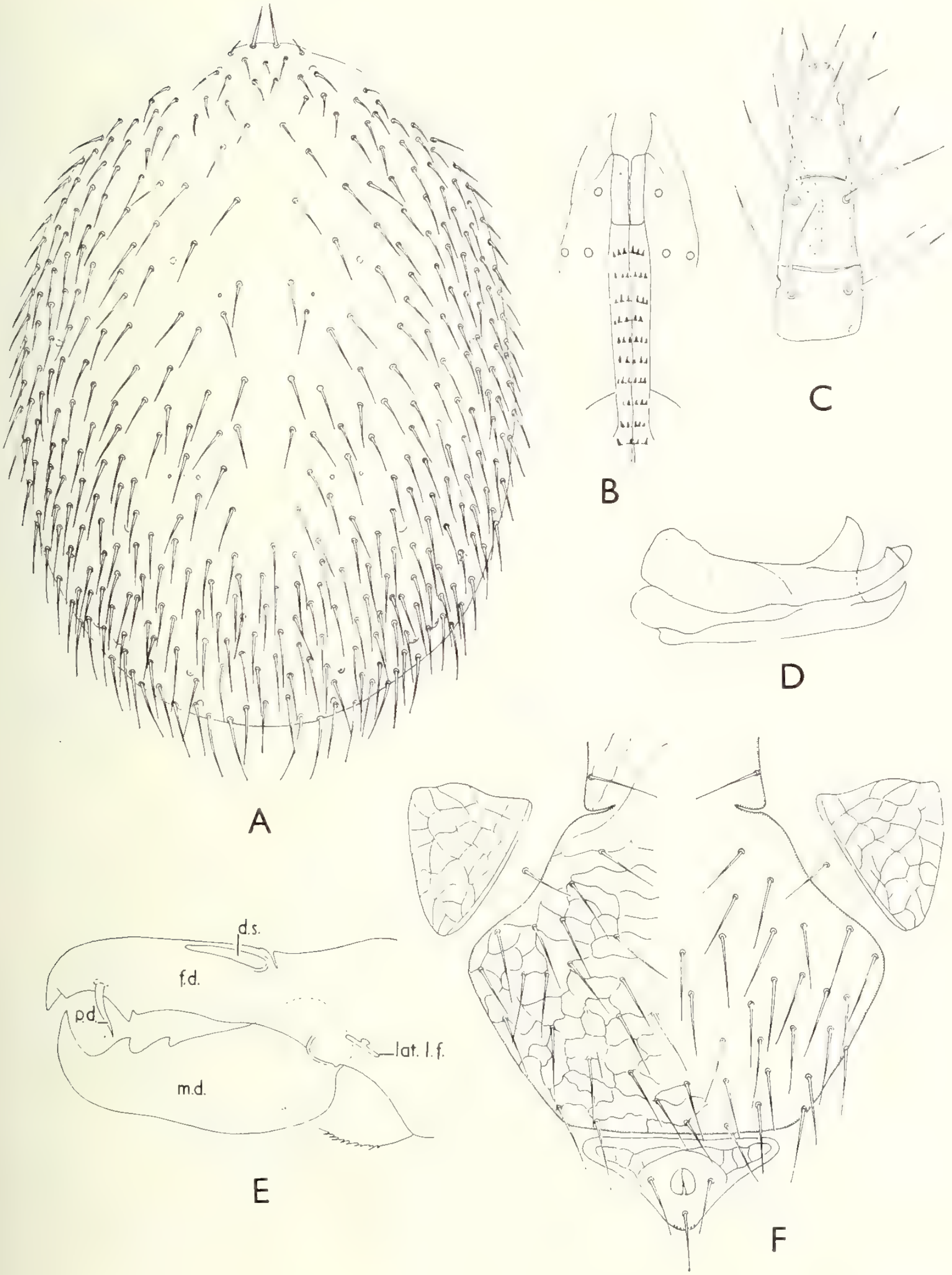


FIG. 61. *Eulaelaps stabularis* (Koch). A. Dorsum of idiosoma of female ; B. deutosternum of female ; C. tarsus II of female ; D. movable digit of chelicera of male ; E. chelicera of female ; F. opisthogastric region of female.

Female: Chelicera with segment I, 90 μ; II, 180 μ; movable digit 75 μ, bidentate; fixed digit tridentate, pilus dentilis short, setiform ; dorsal seta stout (Text-fig. 61E). Four pairs of gnathosomal setae with *c.s.* about 93 μ apart, *hyp.2* about 66 μ apart. Deutosternum (Text-fig. 61B) with ten transverse rows of denticles (4–6 per row) ; corniculi 60 μ long ; internal malae elongate, fringed. Tectum capituli with anterior and lateral margins deeply denticulate. Salivary styli conspicuous, reaching tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele ; palptrochanter with sensory organ ventrally.

Dorsal shield (960 μ × 612 μ) shows marked hypertrichy ; setae simple, mostly subequal, shorter towards anterior margin (Text-fig. 61A). Surface of shield granular and reticulate.

Tritosternum with base 45 μ, laciniae 160 μ ; presternal area well sclerotized. Sternal shield (156 μ × 186 μ) with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between *st1*, 96 μ ; between *st1* and *st3*, 138 μ. Genito-ventral shield (408 μ × 180 μ) with lateral incisions behind the genital setae ; widely expanded behind coxae IV with maximum width 456 μ ; bearing a pair of genital setae and about 47–52 opisthogastric setae (Text-fig. 61F). Anal shield (78 μ × 114 μ) with maximum width at anterior margin 222 μ ; paranal setae 63 μ, postanal seta 78–84 μ long. Metapodal shields very large, subtriangular. Peritreme extends to middle of coxa I ; anterior tip of peritrematal shield fused with dorsal shield at level of seta *z1*, posterior part free.

Chaetotaxy of legs differs from normal pattern in having two postero-lateral setae on genu IV ($2-\frac{2}{1}, \frac{3}{0}-2$). Tarsus II with some spine-like setae (Text-fig. 61C). Some leg segments with distal margins serrate. Length/width (in μ) of leg segments

	I	II	III	IV
genu	138/60	120/78	96/60	132/54
tibia	150/48	114/72	96/54	138/54
tarsus	228/42	156/54	180/48	270/48

Male: Chelicera with segment I, 48 μ ; II, 130 μ ; movable digit 63 μ, with a large, subterminal, tooth-like projection (Text-fig. 61D) ; spermadactyl slightly surpasses tip of movable digit ; fixed digit edentate, pilus dentilis short, setiform. Four pairs of gnathosomal setae with *c.s.* about 54 μ apart, *hyp.2* about 50 μ apart. Deutosternum with nine transverse rows of denticles (4–8 per row) ; corniculi 50 μ long. Internal malae, tectum, salivary styli and pedipalps as in female.

Dorsal shield (582 μ × 348 μ) as in female. Tritosternum with base 30 μ, laciniae 108 μ. Holoventral shield (468 μ × 126 μ) granular and reticulate ; with four pairs of setae and three pairs of pores in the sternal region ; a pair of genitals and 36–43 opisthogastric setae in the genito-ventral region. Between *st1*, 66 μ ; between *st1* and *st3*, 102 μ. Paranal setae 48 μ, postanal seta 60 μ long. Peritreme extends to anterior margin of coxa II ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Chaetotaxy of legs as in female. Femur II with seta v_2 relatively stout, tapering. Setae av_2 and *mv* on tarsus II, seta *av* on genu and tibia II, stout basally, tapering to fine points. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	96/39	75/48	60/36	78/30
tibia	100/36	72/45	57/36	84/30
tarsus	150/30	96/36	105/30	140/27

HABITAT : Found in Britain and Europe on the bodies and in the nests of rodents and insectivores and in the nests of the Wheatear, *Oenanthe oenanthe* Linn. and the Sandmartin, *Riparia riparia* (Linn.).

Eulaelaps novus Vitzthum

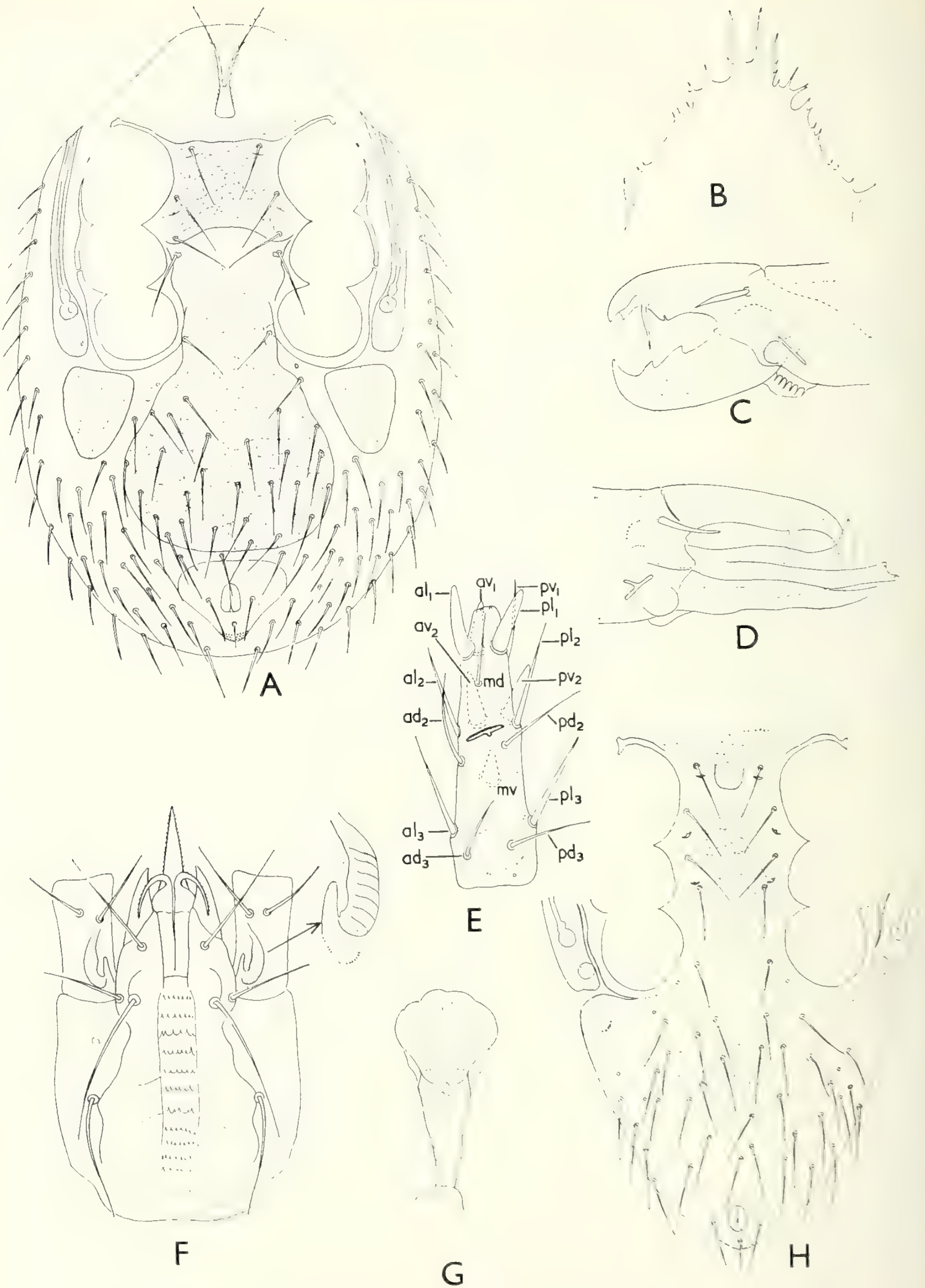
Eulaelaps novus Vitzthum, 1925, *Jen. Z. Naturw.* **62** : 165, fig.
Samsinak, 1960, *Acta Soc. ent. Cech.* **57** : 276, figs.
Eulaelaps kolpakovae Bregetova, 1950, *Parazit. Sb.* **12** : 13, fig. (**syn. nov.**).

Female : Chelicera with segment I, 84 μ ; II, 186 μ ; movable digit 70 μ, bidentate ; fixed digit as in Text-fig. 62C ; pilus dentilis and dorsal seta short, setiform. Four pairs of gnathosomal setae with *c.s.* about 72 μ apart, *hyp.* 2 about 66 μ apart. Deutosternum with eleven transverse rows of denticles (5–7 per row) ; corniculi 50 μ long ; internal malae elongate, fringed (Text-fig. 62F). Tectum capituli with anterior and lateral margins deeply denticulate (Text-fig. 62B). Salivary styli conspicuous, reaching tips of corniculi. Pedipalp (2–5–6–14) with two-tined apotele ; palptrochanter with sensory organ ventrally.

Dorsal shield (936 μ × 588 μ) hypertrichous, surface of shield granular and reticulate. Setae simple, mostly subequal, slightly longer in the opisthonotal region.

Tritosternum with base 63 μ, laciniae 150 μ. Sternal shield (120 μ × 168 μ) with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores on medial margin of setal bases. Between *st*1, 102 μ ; between *st*1 and *st*3, 132 μ. Genito-ventral shield (324 μ × 144 μ) expanded posteriorly with maximum width 300 μ ; bearing a pair of genital and about 26 opisthogastric setae. Anal shield (100 μ × 132 μ) with paranal setae 75 μ, postanal seta 50 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 62A ; metapodal shields large, subtriangular. Peritreme extends to anterior margin of coxa II ; anterior part of peritrematal shield fused with dorsal shield, posterior part free, its pore apparently situated at the bottom of a wide cavity.

Chaetotaxy of legs differs from the normal pattern in that genu IV has two posterolateral setae ($2-\frac{2}{1}, \frac{3}{0}-2$) and tarsi II–IV lack setae ad_1 and pd_1. Tarsus II (Text-fig. 62E) bears several stout, spur-like setae (av_1, al_1, pl_1, av_2, pv_2, *mv*). Ambulacrum I without claws (Text-fig. 62G). Length/width (in μ) of leg segments :


A
B
C
D
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al_1
av_1
pv_1
pl_1
av_2
pl_2
al_2
md
pv_2
ad_2
pd_2
mv
pl_3
al_3
pd_3
ad_3
F
G
H

FIG. 62. *Eulaelaps novus* Vitzthum. A. Venter of idiosoma of female ; B. tectum capituli of female ; C. chelicera of female ; D. chelicera of male ; E. tarsus II of female ; F. venter of gnathosoma of female ; G. ambulacrum of leg I of female ; H. holoventral shield of male.

	I	II	III	IV
genu	126/54	126/72	90/54	132/52
tibia	138/50	108/72	96/54	144/48
tarsus	204/42	150/52	162/45	276/42

Male : Chelicera with segment I, 75 μ ; II, 162 μ ; movable digit 66 μ (81 μ with spermadactyl) ; both digits edentate ; pilus dentilis and dorsal seta as in female (Text-fig. 62D). Four pairs of gnathosomal setae with *c.s.* about 75 μ apart, *hyp.*2 apart 60 μ apart. Deutosternum with 12 transverse rows of denticles (6–10 per row) ; corniculi 36 μ long. Internal malae, tectum, salivary styli and pedipalps as in female.

Dorsal shield (732 μ × 492 μ) as in female. Tritosternum with base 42 μ, laciniae 132 μ. Holoventral shield (576 μ × 135 μ) as in Text-fig. 62H. Between *st*1, 84 μ ; between *st*1 and *st*3, 110 μ. Paranal setae 54 μ ; postanal seta 40 μ. Peritreme extends to middle of coxa II ; anterior part of peritrematal shield fused with dorsal shield ; posterior part free on one side of the only available male, on the other side fused with podal elements of coxa IV and with holoventral shield.

Chaetotaxy of legs as in female. Femur II with large ventral protuberance distal to fissure. Genu and tibia II with setae *av* stout basally. Tarsus II with several stout, blunt setae (av_1, al_1, pl_1, av_2, pv_2) ; seta *mv* stout basally with sharp, tapering point. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	114/48	114/70	84/50	120/48
tibia	120/45	102/60	87/48	126/45
tarsus	186/42	126/40	126/40	234/38

HABITAT : Found in Britain and Europe in the nests of *Riparia riparia* (Linn.). Recorded by Bregetova from the nests of a variety of rodents in the U.S.S.R.

Subfamily **PSEUDOLAELAPINAE** nov.

Adults : Chelicera of both sexes chelate-dentate ; pilus dentilis short, setiform ; dorsal seta and arthrodial processes present ; fissures normal. Male chelicera with spermadactyl grooved, free distally. Chaetotaxy of venter of gnathosoma normal. Pedipalps with five free segments ; chaetotaxy of trochanter to tibia (2–5–6–14) ; apotele two-tined. Deutosternum with seven transverse rows of denticles. Corniculi horn-like, internal malae inflated basally. Tectum captuli trispinate.

Dorsal sclerotization in both sexes comprises an entire shield ; primary chaetotaxy reduced, consisting of 24 pairs of setae.

Tritosternum bipartite, laciniae pilose. Pre-endopodal shields present. Sternal shield in the female with three pairs of setae and two pairs of pores ; metasternal setae on small platelets. Genito-ventral shield inflated, bearing the genital and two pairs of opisthogastric setae. Anal shield with normal chaetotaxy, no euanal setae.

Opisthogastric cuticle sparsely setose. Metapodal shields small, ovoid. Peritrematal shields fused with large podal shields posterior to coxae IV ; peritremes extend beyond coxae I. Male with holoventral shield fused with peritrematal shields ; genital orifice presternal.

All legs six-segmented, with ambulacra and claws. Deviations from normal chaetotaxy occur on genu and tibia I (2—$\frac{3}{1}$, $\frac{3}{1}$—2), genu II (2—$\frac{3}{0}$, $\frac{2}{1}$—2) and genu III (2—$\frac{2}{1}$, $\frac{2}{0}$—1). Coxa II with rounded anterior protuberance.

Immature stages not known.

A single genus.

Genus *PSEUDOLAELAPS* Berlese

Hoplolaelaps Berlese, 1910, *Redia* **6** : 259 (non *Hoplolaelaps* Berlese, 1903).
Pseudolaelaps Berlese, 1916, *Redia* **12** : 30.

Type : *Laelaps* (*Hoplolaelaps*) *doderoi* Berlese, 1910.

With the characters of the subfamily.

Pseudolaelaps doderoi (Berlese)

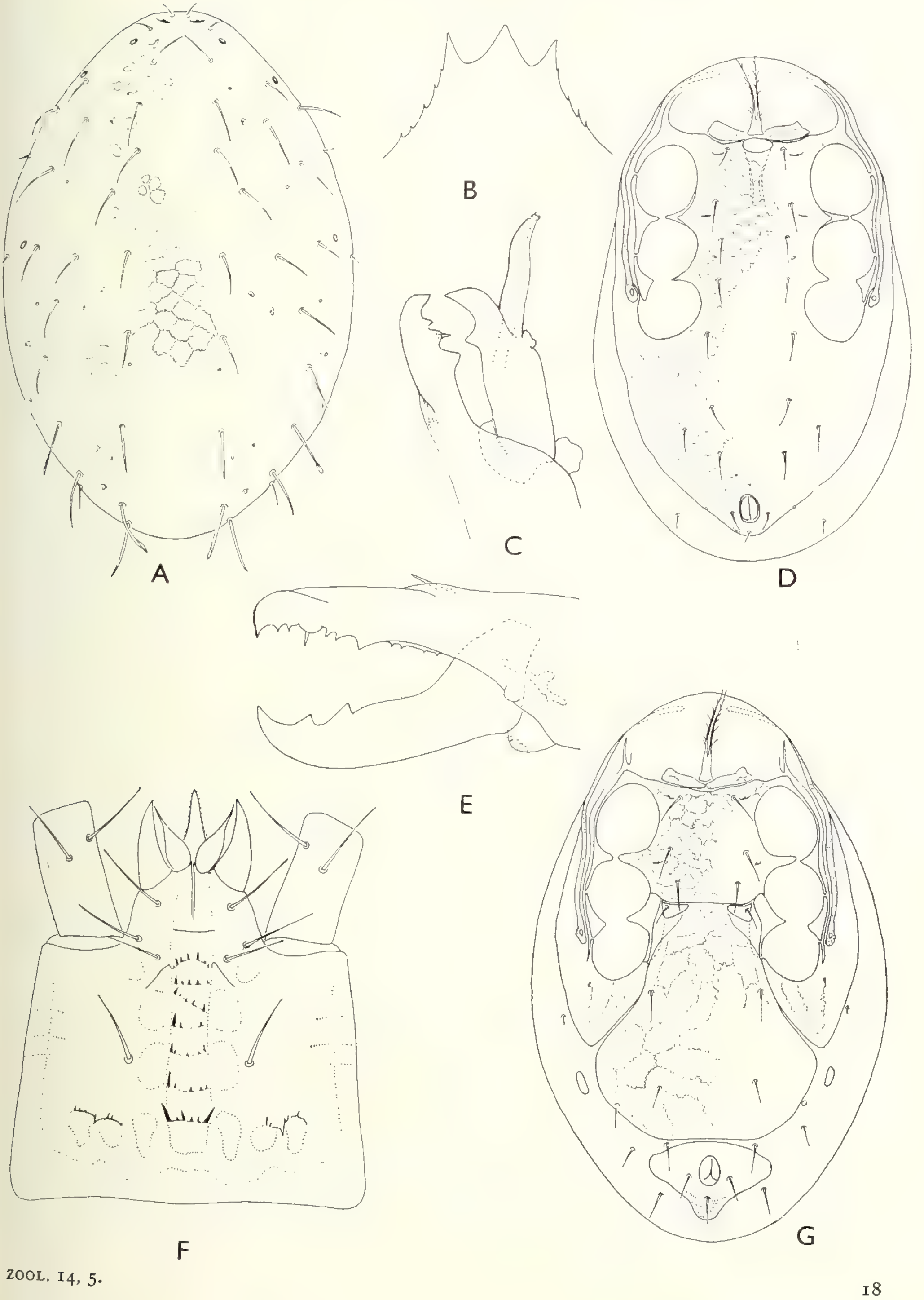
Laelaps (*Hoplolaelaps*) *doderoi* Berlese, 1910, *Redia* **6** : 259.

Female : Chelicera with segment I, 54 μ ; II, 130 μ ; movable digit 50 μ, bidentate ; fixed digit with about nine teeth, pilus dentilis short, setiform ; dorsal seta nearly half-way towards apex of digit (Text-fig. 63E). Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with seven transverse rows of denticles (3 to 7 denticles per row) ; a row of small denticles postero-lateral to the capitular setae ; corniculi 33 μ long, horn-like ; internal malae broad basally, tapering to fine points (Text-fig. 63F). Tectum capituli trispinate, lateral margins denticulate (Text-fig. 63B). Pedipalps (2–5–6–14) with two-tined apotele.

Dorsal shield (474 μ × 318 μ) with 24 pairs of setae distributed as in Text-fig. 63A, some posterior setae paddle-shaped. Surface of shield reticulate.

Tritosternum with base 27 μ, laciniae 70 μ. Sternal shield (100 μ × 110 μ) with three pairs of setae and two pairs of pores ; metasternal setae on small shields, associated pores not visible. Between *st*1, 48 μ ; between *st*1 and *st*3, 78 μ. Genito-ventral shield (135 μ × 100 μ) greatly expanded posteriorly, with a pair of genital and two pairs of opisthogastric setae ; greatest width of shield about 204 μ. Anal shield (48 μ × 108 μ) with paranal setae 18 μ, postanal seta 15 μ long. Chaetotaxy

FIG. 63. *Pseudolaelaps doderoi* Berlese. A. Dorsum of idiosoma of female ; B. tectum capituli of female ; C. chelicera of male, internal view ; D. venter of idiosoma of male ; E. chelicera of female, internal view ; F. venter of gnathosoma of female ; G. venter of idiosoma of female.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and sclerotization of opisthogaster as in Text-fig. 63G. Peritreme extends beyond lateral margin of gnathosoma ; peritrematal shield fused with large metapodal shield.

Chaetotaxy of legs differs from normal pattern on genu and tibia I $(2-\frac{3}{1}, \frac{3}{1}-2)$, genu II $(2-\frac{3}{0}, \frac{2}{1}-2)$, and genu III $(2-\frac{2}{1}, \frac{2}{0}-1)$. Coxa II has a rounded anterior protuberance. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	66/24	54/30	42/24	60/27
tibia	63/18	54/30	45/27	72/24
tarsus	108/15	117/24	108/24	170/20

Male : Chelicera with segment I, 42 μ ; II, 100 μ ; movable digit 42 μ (54 μ with spermadactyl), unidentate ; fixed digit with two teeth and a minute, setiform, pilus dentilis on a small, tooth-like projection (Text-fig. 63C). Four pairs of gnathosomal setae with *c.s.* about 36 μ apart ; *hyp.*2 about 30 μ apart. Deutosternum with six transverse rows of denticles (two to several per row) ; a row of small denticles posterolateral to setae *c.s.* Corniculi 30 μ long ; internal malae, tectum and pedipalps as in female.

Dorsal shield (354 μ × 246 μ) with 24 pairs of setae as in female. Tritosternum with base 12 μ, laciniae 57 μ. Holoventral shield (282 μ × 90 μ) with four pairs of setae and three pairs of pores in the sternal region, four pairs of setae in the genitoventral region (Text-fig. 63D). Between *st*1, 40 μ ; between *st*1 and *st*3, 66 μ. Paranal setae 15 μ, postanal seta 12 μ long. Peritreme as in female, peritrematal shield fused with holoventral shield.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	54/20	48/27	40/24	50/20
tibia	57/18	45/27	40/24	60/20
tarsus	90/15	90/20	90/20	144/18

HABITAT : Recorded in Britain from the soil of a grassy bank, London, and from an arable field on clay/chalk, Winchester, Hampshire. Originally found in soil in Italy.

Subfamily **MYONYSSINAE** Bregetova

Myonyssinae Bregetova, 1956, *Opred. Faune SSSR.* **61** : 52.

Adults : Chelicerae essentially edentate, fixed digit long and slender in both sexes and in the female it may have a small dorsally directed tooth. Spermadactyl relatively short, grooved, and entirely fused with the movable digit. Pilus dentilis and dorsal seta apparently absent, fissures inconspicuous, arthrodial processes absent. Chaetotaxy of venter of gnathosoma normal ; pedipalps with five free segments and a two-tined apotele, chaetotaxy normal (2–5–6–14). Deutosternum with 9–12 denticles arranged in a single file. Corniculi horn-like, relatively weakly slcerotized ; internal malae long, simple. Salivary styli massive. Tectum capituli elongate, tapering distally and with a smooth margin.

Dorsal shield entire in both sexes ; in the female typically with 38 pairs of setae comprising 21 pairs of podonotals (*z*2 lacking) and 17 pairs of opisthonotals (*px*2 and *px*3 present). Sometimes normal complement decreased (*M. montanus*) by the absence of *px*2, *px*3 and *S*3 on the opisthonotal region. Dorsal shield in the males of two main types, one in which the chaetotaxy resembles that of the female (*M. montanus* group), and the other in which the female complement is increased by the incorporation of certain of the *r* and *R* setae on the lateral margins of the shield (*M. gigas* group). Sexual dimorphism is evident in the second type, by the extreme length of certain of the setae on the posterior region of the shield.

Tritosternum bipartite, base lacking hyaline denticulate border. Sternal shield well-sclerotized, reticulate, slightly wider than long and bearing three pairs of setae and two pairs of pores. Genito-ventral shield large, flask-shaped, with from 4–22 setae excluding the genitals. Anal shield with normal three setae, rarely with an additional unpaired accessory seta, and considerably wider than long. Metapodals present. Opisthogastric cuticle with varying degrees of hypertrichy. Peritrematal shields free posteriorly. Male with holoventral shield free from peritrematal shields and with hypertrichy of the ventral region.

Chaetotaxy of legs normal. Coxa II usually with prominent anterior spine. All ambulacra with well-developed claws.

Larva and Protonymph : Apparently unknown.

Deutonymph : Active feeding instar. Gnathosoma with characteristics of female. Dorsal shield with lateral incisions ; chaetotaxy of the dorsum as in the female, but fewer setae situated on the dorsal shield. Tritosternum bipartite, pilose. Sternito-genital shield with sternal setae 1–3 ; metasternals and genitals flanking the shield. Anal shield similar in shape to that of female ; chaetotaxy of opisthogaster as in adult. Peritremes shorter than in the adult. Leg chaetotaxy normal.

Genus ***MYONYSSUS*** Tiraboschi

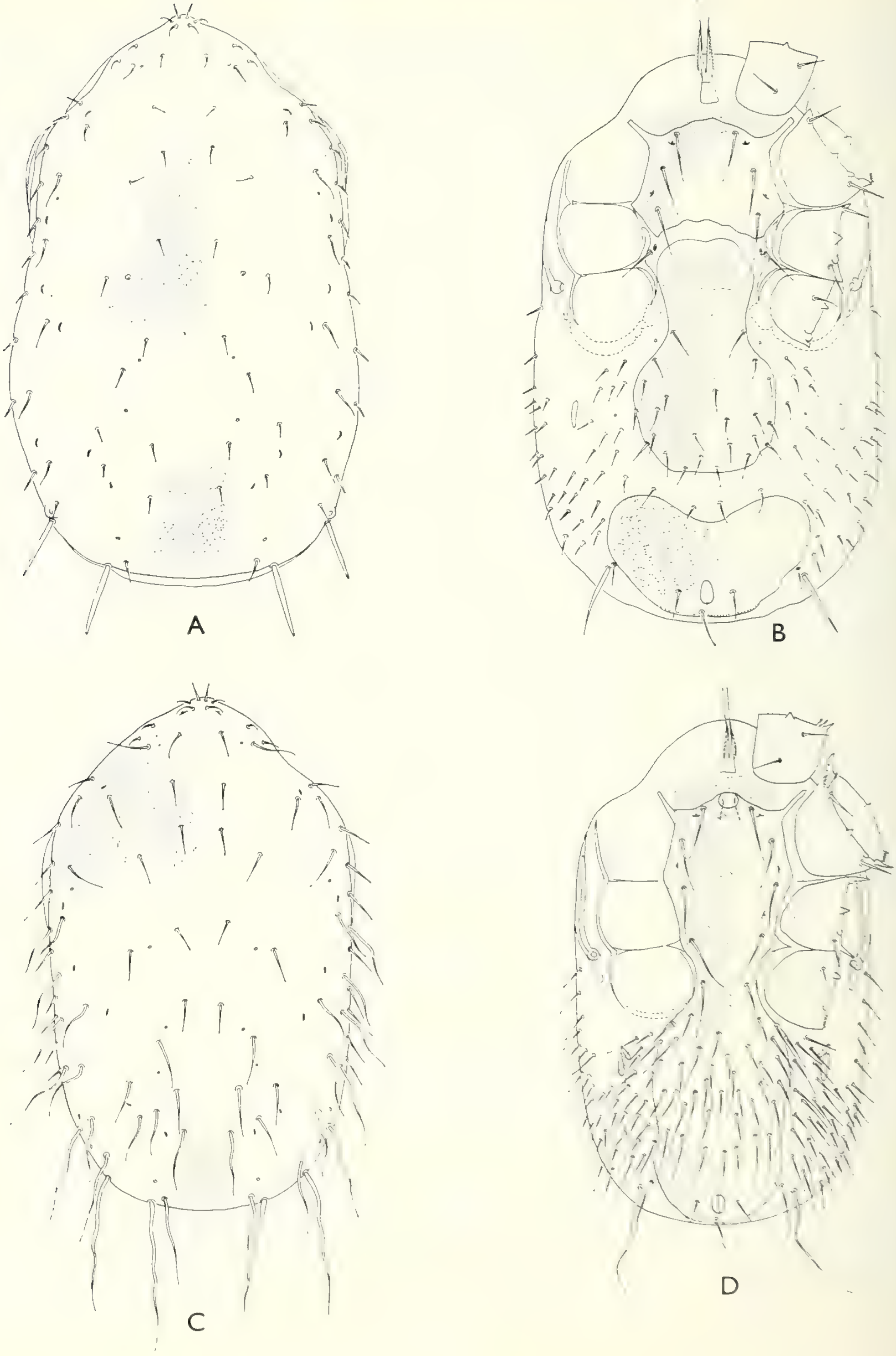
Myonyssus Tiraboschi, 1904, *Arch. Parasit.* **8** : 337.
Tetragonyssus Ewing, 1923, *Proc. U.S. nat. Mus.* **62** (art. 13) : 6.

Type : *Myonyssus decumani* Tiraboschi, 1904.

The genus has the characters of the subfamily as diagnosed above.

KEY TO FEMALES

Genito-ventral shield with less than 12 setae ; anal shield about 1½ times as broad as long . . . . **M. decumani** Tiraboschi (p. 271)
Genito-ventral shield with about 20 setae (Text-fig. 64B) ; anal shield about twice as broad as long . . . . **M. gigas** (Oudemans) (p. 271)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Myonyssus decumani Tiraboschi

Myonyssus decumani Tiraboschi, 1904, *Arch. parasit.* **8** : 337 ; Hirst, 1916, *J. zool. Res.* **1** : 64, figs.

We have not examined specimens of this species which is adequately described and figured by Hirst (1916).

HABITAT : The only British records of the species are from a house mouse (*Mus musculus* Linn.) at Ollaberry, Shetland Islands (Hirst, 1916).

Myonyssus gigas (Oudemans)

Liponyssus gigas Oudemans, 1912, *Ent. Ber. Amst.* **3** : 231.
Myonyssus gigas: Bregetova, 1956, *Opred. Faune SSSR.* **61** : 123, figs. 243, 251.

Female: Chelicera with segment I, 48 μ; II 189 μ ; movable digit 57 μ, edentate; fixed digit unidentate (Text-fig. 65A and B) ; pilus dentilis absent. Four pairs of gnathosomal setae with *c.s.* about 72 μ apart, *hyp.*2 about 54 μ apart. Deutosternum with eleven denticles arranged in a single file ; corniculi 45 μ long, weakly sclerotized ; internal malae elongate (Text-fig. 65C). Salivary styli conspicuous, extending well beyond tips of corniculi. Tectum capituli triangular with smooth margin (Text-fig. 65D). Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (1,140 μ × 636 μ) with 38 pairs of setae distributed as in Text-fig. 64A ; seta *z*2 is absent. Setae *Z*5 and *S*5 considerably longer than the other setae and very stout and blade-like. Surface of shield reticulate with a granular pattern posteriorly ; no hypertrichy.

Tritosternum with base 70 μ, laciniae 170 μ. Sternal shield (210 μ × 252 μ) with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores ; between *st*1, 120 μ ; between *st*1 and *st*3, 174 μ. Genital shield (282 μ × 160 μ) flask-shaped with one pair of genital setae and about 22 opisthogastric setae which are not strictly symmetrical in their arrangement (Text-fig. 64B). Anal shield (186 μ × 294 μ) with deeply concave anterior margin and maximum width 408 μ. Paranal setae 60 μ, postanal seta 66 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 64B. Peritreme extends to posterior third of coxa II ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Legs with normal chaetotaxy. Coxae II–IV are provided with spurs, as shown in Text-fig. 64B. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	144/96	144/102	120/90	150/84
tibia	135/84	108/96	108/84	150/84
tarsus	174/70	144/72	168/70	216/72

FIG. 64. *Myonyssus gigas* (Oudemans). A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. dorsum of idiosoma of male ; D. venter of idiosoma of male.

Male : Chelicera with segment I, 60 μ ; II, 180 μ ; movable digit 80 μ, both digits edentate (Text-fig. 65E). Four pairs of gnathosomal setae with *c.s.* about 72 μ apart, *hyp.*2 about 57 μ apart. Deutosternum, internal malae, salivary styli, tectum and pedipalps as in female. Corniculi 54 μ long, slender, weakly sclerotized.

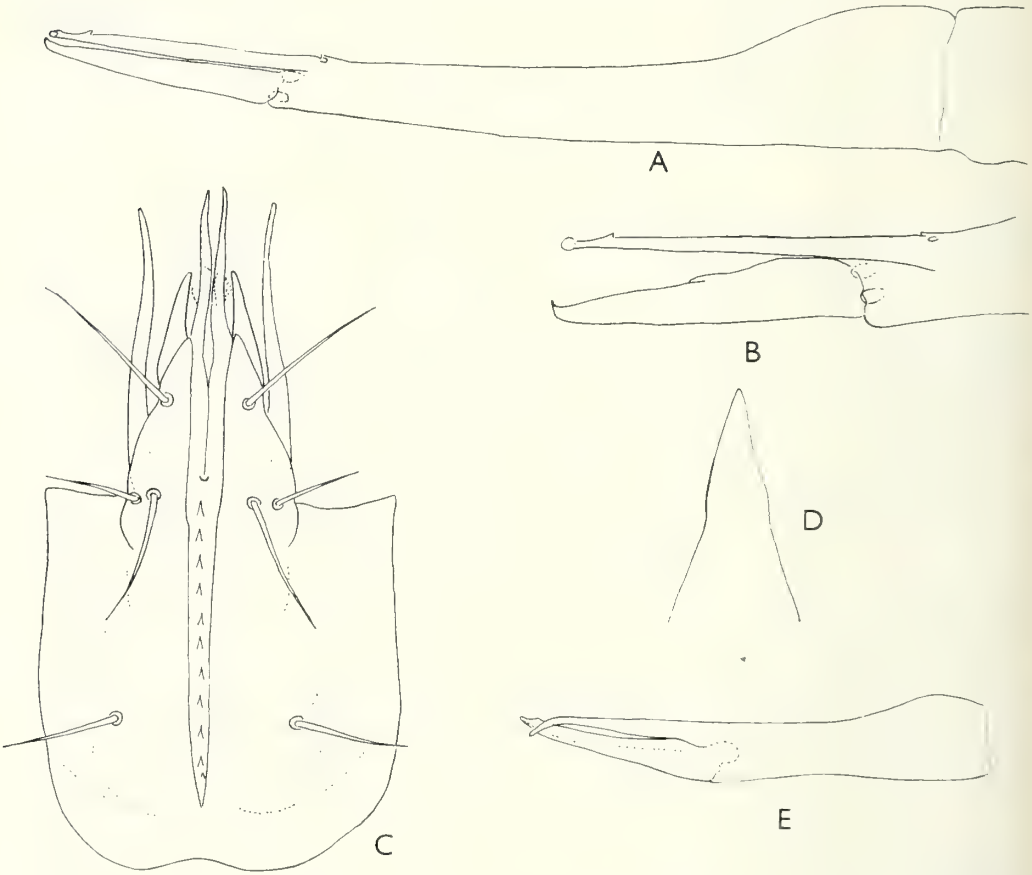

FIG. 65. *Myonyssus gigas* (Oudemans). A–B. Chelicera of female ; C. venter of gnathosoma of female ; D. tectum capituli of female E. chelicera of male.

Dorsal shield (1,188 μ × 684 μ) with 21 pairs of setae in the podonotal region, as in the female, whereas the opisthonotal region bears 22 pairs of setae, five marginal pairs being included on the shield (Text-fig. 64C). The setae are relatively longer than in the female and some, particularly the *Z* and *S* series and *J*4–5, are sinuous.

Tritosternum with base 36 μ, laciniae 174 μ. Holoventral shield (984 μ × 270 μ) with four pairs of setae and three pairs of pores in the sternal region and numerous setae in the genito-ventral region. Between *st*1, 114 μ ; between *st*1 and *st*3, 108 μ. Paranal setae 60 μ, postanal seta 78 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 64D. Peritreme extends to posterior third of coxa II ; anterior part of peritrematal shield fused with dorsal shield, posterior part free.

Legs with normal chaetotaxy. Coxae I–IV provided with spurs, as shown in Text-fig. 64D. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	168/108	168/132	144/114	192/117
tibia	162/96	138/120	126/102	180/110
tarsus	192/84	174/84	180/78	264/87

HABITAT : Found on moles (*Talpa europaea* Linn.) and in their nests, and on field mice [*Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linn.)] in Britain and Europe.

Subfamily **MELITTIPHINAE** nov.

Adults : Chelicerae in the female chelate, fixed digit essentially edentate, movable digit weakly bidentate. Chelicerae of male strongly modified ; fixed digit reduced ; movable digit fused with long, slender, grooved spermadactyl. Pilus dentilis present in female ; dorsal seta and fissures normal ; arthrodial processes present, at least in female. Chaetotaxy of venter of gnathosoma and pedipalps normal. Apotele two-tined. Deutosternum with about eight denticles in a single file. Corniculi slender, horn-like ; internal malae long, bipartite anteriorly. Tectum capituli with smooth, rounded, anterior margin.

Dorsum of idiosoma entirely covered by a single shield, hypertrichy obscuring the primary chaetotaxy. Certain marginal setae subspinose.

Tritosternum bipartite, normal. Presternal area moderately sclerotized, with a median keel-like ridge. Sternal shield in female with three pairs of setae and two pairs of pores. Genital shield flask-shaped with genital setae only. Anal shield ovoid, with aciculated portion bent dorsally, resulting in posterior margin of shield appearing concave. Anus situated in posterior third of shield ; a posteriorly directed spur present immediately anterior to the anus. Opisthogastric cuticle hypertrichous. Peritrematal shields free posteriorly. Male with a sternito-genital and a ventro-anal shield.

Chaetotaxy of legs normal except tibia III ($2—\frac{1}{1}, \frac{2}{1}—2$) and genu IV ($2—\frac{2}{1}, \frac{3}{1}—1$). Coxa II with complex anterior spine (Text-fig. 66C). All ambulacra with a pair of claws.

The genus *Melittiphis* was previously placed in the family Eviphididae, on the basis of Vitzthum's (1930) description of the tectum capituli, namely : " Epistom dem *Iphis*-Typus entsprechend eine langgezogene Spitze, beiderseits und dorsal fein gezähnelt ". This description refers to the labrum and not to the tectum (see Text-fig. 66B).

Immature stages not known.

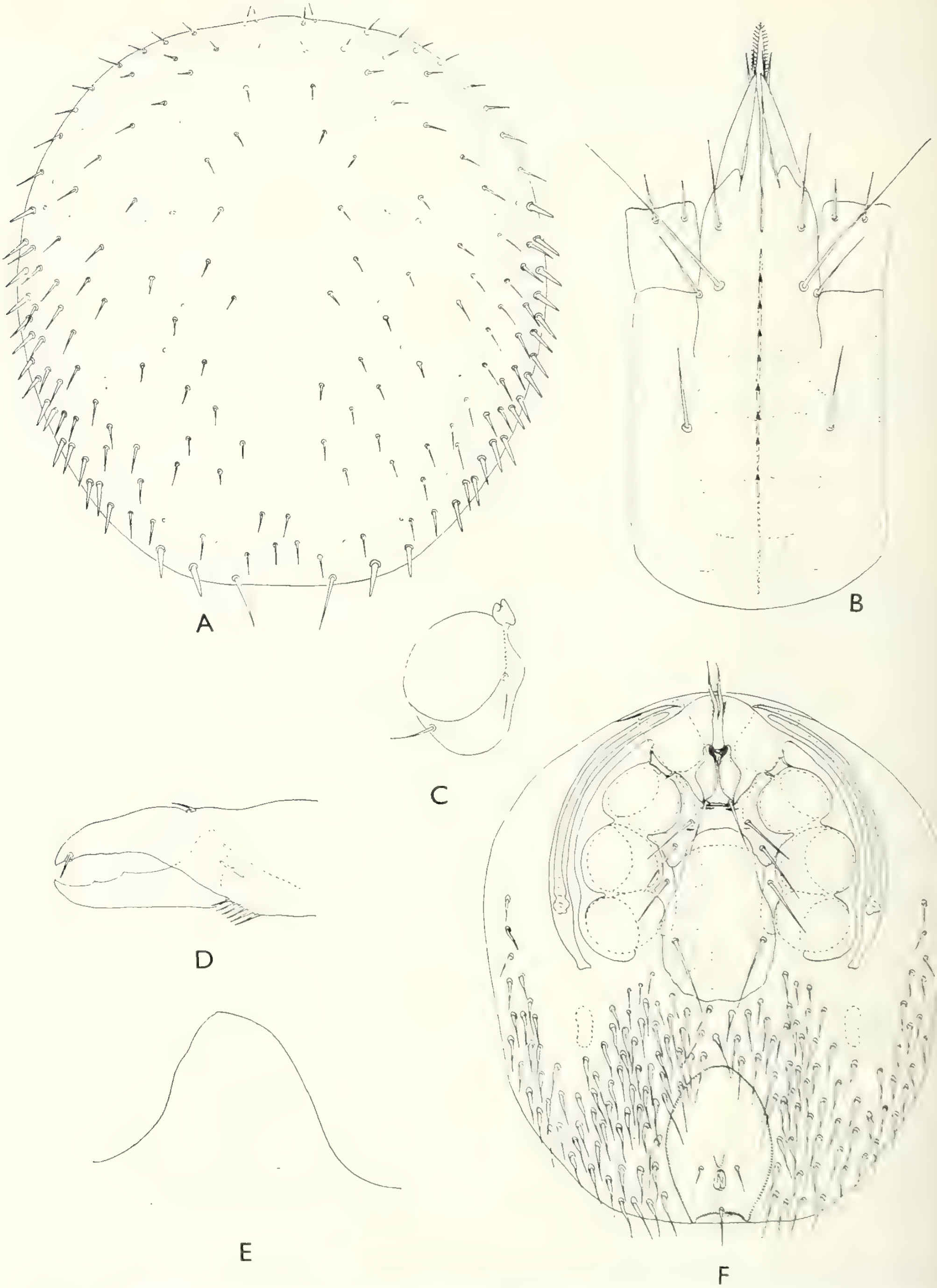

Fig. 66. *Melittiphis alvearius* (Berlese), female ; dorsum of idiosoma (A) ; venter of gnathosoma (B) ; coxa II (C) ; chelicera (D) ; tectum capituli (E) ; venter of idiosoma (F).

Genus *MELITTIPHIS* Berlese

Melittiphis Berlese, 1918, *Redia* **13** : 117.

Type : *Laelaps* (*Iphis*) *alvearius* Berlese, 1896.

The genus has the characters of the subfamily as diagnosed above.

Melittiphis alvearius (Berlese)

Iphis alvearius Berlese, 1896, *Atti Soc. Veneto-Trent.* (2) **2** : 318.

Female : Chelicera with segment I, 48 μ ; II, 115 μ ; movable digit 45 μ, weakly bidentate ; fixed digit edentate, pilus dentilis and dorsal seta short, setiform (Text-fig. 66D). Four pairs of gnathosomal setae with distance between *c.s.* slightly exceeding distance between *hyp.2*. Deutosternum with eight denticles arranged in a single file ; corniculi 36 μ long, converging; internal malae elongate, bipartite anteriorly (Text-fig. 66B). Tectum capituli with anterior margin smooth (Text-fig. 66E). Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (780 μ × 660 μ) shows marked hypertrichy ; marginal setae relatively stout and spine-like (Text-fig. 66A). Surface of shield reticulate.

Tritosternum with laciniae about three times as long as the base. Sternal shield (75 μ × 80 μ) with three pairs of setae and two pairs of pores ; metasternal setae situated over the endopodal shields. Between *st*1, 30 μ ; between *st*1 and *st*3, 78 μ. Genital shield (90 μ × 147 μ) with genital setae only. Anal shield (204 μ × 138 μ) with paranal setae 40 μ, postanal seta 48 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 66F. Peritreme extends nearly to anterior margin of coxa I ; anterior part of peritrematal shield fused with dorsal shield at level of seta *z*2, posterior part free.

Chaetotaxy of legs differs from normal pattern in that tibia III has two posterolateral setae ($2-\frac{1}{1}, \frac{2}{1}-2$), genu IV has two ventral setae ($2-\frac{2}{1}, \frac{3}{1}-1$), tarsi II–IV lack setae ad_1 and pd_1. Stout spine-like setae are present on femur II (ad_1, pd_1, pl_1 and v_3) ; trochanter III (*al*) ; femur III (distal dorsal) ; genu III (ad_1) ; trochanter IV (*al*) ; femur IV (distal dorsal) ; genu IV (ad_{1-2}). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	72/45	84/70	63/57	75/54
tibia	72/36	60/54	54/48	66/48
tarsus	138/36	135/42	144/42	168/42

Male : Certain details of the morphology of the male, given in the subfamilial diagnosis, have been obtained from a specimen in the Berlese collection, Florence.

Habitat : Found in bee-hives in Britain and Europe.

Subfamily **HIRSTIONYSSINAE** nov.

Adults : Chelicerae in female chelate-edentate, movable digit rarely bidentate or weakly dentate ; fixed digit with hyaline process which may be produced distally into a slender lobe (*Patrinyssus*). Male with relatively short, grooved spermadactyl usually completely fused with the movable digit ; fixed digit edentate. Pilus dentilis apparently absent, dorsal seta reduced to microseta or absent, fissures present, arthrodial processes reduced or absent. Chaetotaxy of venter of gnathosoma normal. Pedipalpal chaetotaxy normal or femur unideficient, genu unideficient, or tibia uni- or bideficient ; apotele simple (*Patrinyssus*) or two-tined. Palptrochanter rarely with ventral keel produced posteriorly into a spur (*Trichosurolaelaps*). Deutosternum with five to 18 transverse rows of denticles, transverse rows comprising one to four denticles. Hypostome elongate, internal malae simple, often long ; corniculi membranous, rarely with horn-like apex. Tectum capituli tongue-like, with anterior margin smooth or fimbriated.

Dorsum with entire shield in both sexes, bearing 22–27 pairs of setae in the female, never holotrichous ; setae *z*1 rarely present, *J* series showing hypotrichy, *J*5 present or absent ; opisthonotal region of shield with less than 15 pairs of setae in the female. Sexual dimorphism apparent in the relative lengths of the lateral and marginal setae, those of the male being considerably longer than in the female. Dorsal setae simple.

Tritosternum normal, bipartite, laciniae smooth or pilose, without hyaline denticulate margins. Sternal shield in female with three pairs of setae and two pairs of pores ; metasternals free. Genital shield tongue-shaped, normally bearing only the genital setae. Anal shield normal, opisthogastric cuticle with a variable number of setae which may be affected by sexual dimorphism. Metapodal shields weakly developed or absent. Peritrematal shields free or fused posteriorly with the podal shields. Stigmatal atrium normal or greatly enlarged, peritremes often reduced. Podal shields poorly developed posterior to coxae IV. Male with holoventral shield not fused with peritrematal shields ; rarely with division or weaker sclerotized region between the ventral and anal portions of the shield. Genital orifice presternal.

Chaetotaxy of legs normal (*Hirstionyssus*) or with deficiencies in the chaetotaxy of genua and tibiae III and IV. Anterior spine of coxa II well developed or absent (*Patrinyssus*), that of *Echinonyssus* greatly enlarged and hook-like. One or more of the coxae with a distinct, non-setigerous spur or spurs (excluding anterior spine of coxa II). Certain coxal setae and ventral setae of tibiae and genua may be hypertrophied and form retrograde spurs. Ambulacra with well-developed claws. Male with thumb-like ventral spur on femur II in some *Echinonyssus*.

Immature stages : The larval and protonymphal stages have been described only for *Hirstionyssus* (Bregetova, 1956). The larva is apparently non-feeding and has weakly developed chelicerae with minute digits. On the other hand, the protonymph is probably a feeding stage although the form of the chelicerae is not shown in detail by Bregetova. It lacks distinct dorsal and ventral sclerotization. All known deutonymphs are feeding stages with the general characteristics of the female except for the intercoxal region which has a sternito-genital shield bearing four pairs of setae ; the genital setae flank the shield in the region of coxae IV.

This subfamily is represented in the British fauna by the genus *Hirstionyssus*.

Genus ***HIRSTIONYSSUS*** Fonseca

Hirstionyssus Fonseca, 1948, *Proc. zool. Soc. Lond.* **118** : 266.

Type : *Hirstionyssus talpae* Zemskaya, 1955 (= *Hirstionyssus arcuatus* (Koch) Fonseca, 1948).

Medium sclerotized mites ranging from 450 μ to 950 μ in length. Chelicerae chelate-edentate in both sexes ; fixed digit in the female with membranous sheath. Movable digit in male completely fused with the deeply grooved spermadactyl. Pilus dentilis apparently absent ; dorsal seta reduced to microseta or absent ; fissures present. Arthrodial processes at base of movable digit reduced or absent. Chaetotaxy of venter of gnathosoma normal ; pedipalpal chaetotaxy normal (2–5–6–14), or palp-tibia unideficient (2–5–6–13) or bideficient (2–5–6–12), apotele two-tined. Palp-trochanter without ventral keel. Deutosternum with 11 to 18 rows of denticles, each row comprising one to four denticles. Internal malae simple, variable in length ; corniculi membranous, never horn-like. Salivary styli strong. Tectum capituli elongate, tongue-shaped, with anterior margin smooth or fimbriated.

Dorsum of idiosoma with entire shield bearing 23 to 27 pairs of setae ; *z*1 never present. Chaetotaxy of opisthonotal region may show intraspecific variation. Unpaired accessory setae never present.

Tritosternum normal, bipartite. Sternal shield in female with three pairs of setae and two pairs of pores. Genital shield tongue-shaped, bearing one pair of genital setae only. Pear-shaped anal shield with normal chaetotaxy, paranal setae approximately level with or behind anterior margin of anus. Opisthogastric cuticle with a variable number of setae which may be affected by sexual dimorphism. Peritrematal shields free or fused posteriorly with the podal shields. Metapodal shields weakly developed or absent. Male with holoventral shield not fused with peritrematal shields, and bearing eight pairs of setae excluding the anals. Podal shields poorly developed posterior to coxae IV.

Chaetotaxy of legs normal. At least one of the coxae provided with non-setigerous spurs, apart from the anterior spine of coxa II. All ambulacra with a pair of well-developed claws.

As in many other genera of obligatory ectoparasitic dermanyssid mites, there is considerable confusion in the literature concerning the nomenclature and systematic position of certain of the " older " species. This is particularly evident in the genus *Hirstionyssus* and concerns, in the present study, the species *Hirstionyssus arcuatus* (Koch) and *musculi* (Johnston). The confusion has arisen largely from Oudemans' concept of the species *Dermanyssus arcuatus* Koch, *Acarus musculi* Schrank and *Dermanyssus musculi* Koch.

The type host of *D. arcuatus* is the chiropteran " *Vespertilio noctula* ", but the original description and illustration of the species are inadequate for its specific identity. Berlese (1889), following Canestrini 1885, attributed *arcuatus* [*Leiognathus arcuatus* (K.) Can.] to a species of dermanyssine mite commonly found on vespertilionid bats (particularly " *V. noctula* ") and his figures and description leave one in no doubt that he considered *arcuatus* to be a member of the genus *Steatonyssus* (probably *S. periblepharus* Kolenati) in its present concept. However, Oudemans (1913), without reference to Berlese or Canestrini, considered *Dermanyssus arcuatus* Koch, which he transferred to the genus *Liponyssus*, to be conspecific with a dermanyssine mite associated with *Talpa* and gave a comprehensive description, with figures, of this mole mite. Unfortunately subsequent workers, excluding Zemskaya and Bregetova in the U.S.S.R., have accepted Oudemans' concept of *arcuatus* and Fonseca (1948)[7] proposed the genus *Hirstionyssus* to accommodate the type *Hirstionyssus arcuatus* (Koch, 1839) and several congeneric species. *Hirstionyssus arcuatus* (Koch) Fonseca, 1948, and its congeners are essentially ectoparasites of Insectivora, Carnivora, Lagomorpha and Rodentia; there are no authenticated records of any *Hirstionyssus* species from Chiroptera. Thus, there can be no doubt that *H. arcuatus* sensu Fonseca 1948 and Oudemans 1913, is neither conspecific nor congeneric with *Dermanyssus arcuatus* Koch, 1839 and, in our opinion, Zemskaya (see Bregetova, 1956) was correct in proposing the name *Hirstionyssus talpae* for *Liponyssus arcuatus* sensu Oudemans, 1913 [= *Hirstionyssus arcuatus* (Koch) Fonseca]. *Hirstionyssus talpae* Zemskaya, 1955, becomes the type of the genus *Hirstionyssus* Fonseca.

Strandtmann & Wharton (1958) have continued to use *Hirstionyssus arcuatus* (Koch) sensu Oudemans 1913 and their synonymy of the species and list of hosts demonstrate the utter confusion surrounding this name. The synonyms *Dermanyssus albatus* Koch, 1839, *Dermanyssus noctula* Koch, 1839 (teste Oudemans, 1936) and *Dermanyssus pipistrellae* Gervais, 1841, are all bat mites and probably belong in the Macronyssinae whilst the host list contains several species of Chiroptera, *Putorius erminea*, as well as *Talpa europaea* and many Rodentia. There is little point in attempting to conserve *Hirstionyssus arcuatus* under these conditions. We strongly advise for the sake of nomenclatural stability the acceptance of *Hirstionyssus talpae* for *Hirstionyssus arcuatus* Oudemans non Koch, 1839, and the removal of *Dermanyssus arcuatus, albatus* (based on a protonymph), *noctulae* and *pipistrellae* from *Hirstionyssus* to the subfamily Macronyssinae where they can remain as species incertae sedis. Reference to Chiroptera as hosts of *Hirstionyssus* should in future be excluded unless, of course, the record can be authenticated.

Till & Evans (1964) have already commented on Oudemans' concepts of *Dermanyssus musculi* Koch 1839 and have shown that at one time or another he considered the species to be congeneric with *Steatonyssus, Macronyssus* and *Ornithonyssus*. His final opinion appears to be expressed in the " *Kritisch Historisch Oversicht der Acarologie* " (1936) where he considered *D. musculi* to be synonymous with *Acarus musculi* Schrank 1803 and referred both to the genus *Steatonyssus*. Both Schrank and Koch recorded their species from the house mouse (*Mus musculus*) and since there have never been any confirmed records of species of the genus *Steatonyssus* from this host (or from any other rodent for that matter), it seems almost certain that Schrank's and Koch's mites do not belong to this genus. Zemskaya (1955) and Bregetova (1956) who were the first to examine critically the old "*Hirstionyssus arcuatus* complex" showed that the species occurring on *Talpa* was not conspecific with the species parasitizing *Mus, Rattus* and *Apodemus*, for which they adopted the name *Hirstionyssus musculi* (Johnston). In our opinion this name cannot be used for this species for the following reasons :

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[7] Fonseca states: " *Hirstionyssus*, gen. nov., here created to include numerous species related to *Dermanyssus arcuatus* Koch, 1839 (= *Liponyssus arcuatus* auct.) parasites on Chiroptera, Rodentia etc. . . . Genotype *Hirstionyssus arcuatus* (Koch, 1839) ".

1. Johnston (1849) described his species under the name *Dermanyssus musculi* and indicated that he considered it to be conspecific with *D. musculi* Koch by referring to "*Dermanyssus musculi*, Koch Uebers. Arachnid p. 81 tab. 9 fig. 46" immediately after his Latin diagnosis of the species. If Johnston's species is not conspecific with *D. musculi* Koch, as Zemskaya and Bregetova infer, then they should have used the combination *Hirstionyssus johnstoni* (Oudemans, 1936) [= *Macronyssus johnstoni* Oudemans nom. nov. pro *Dermanyssus musculi* Johnston 1849 non Koch 1836] and not *Hirstionyssus musculi* (Johnston).
2. It is clear from Johnston's description that his species was not a *Hirstionyssus*; for example, its size is stated to be equal to *Gamasus coleoptratorum* (whose nymphs measure about 1,000 μ in length), the body is thickly covered with very short, adpressed, somewhat curved bristles and the "bristles" of the legs are stated to be "setaceous, pointed downwards, longer than the diameter of the joint, barbed with minute spinules on one side". Johnston's mite was probably a species of *Haemogamasus*.

The original descriptions of the colour of the idiosoma of *Acarus musculi* Schrank and its synonym *Dermanyssus musculi* Koch indicate that the species is a haematophagous, obligatory ectoparasite. Schrank's "braunroth . . . und das Vorderende weisslicht" and Koch's "Der Vorderleib rein weiss, ein Schiefleck, von den Seiten bis zum Hinterrande reichend dunkelroth, dazwischen ein herzförmiges Fleckchen hellroth" could refer to engorged forms of both *Hirstionyssus* and *Ornithonyssus* in which the general brownish-red colouration of the idiosoma does not extend to the anterior region, the colour pattern being determined by the blood-containing diverticula of the "stomach". The description of the first pair of legs—"Fusspaar etwas länger und schmäler"—by Schrank and the form of these appendages in Koch's illustration of the species excludes the possibility that *A. musculi* is a *Hirstionyssus* and supports our previous suggestion that the species "might possibly be conspecific with *O. bacoti*" (Till and Evans, 1964).

Hirstionyssus musculi (Johnston) Bregetova appears to be conspecific with at least two, possibly three, presently considered valid species of *Hirstionyssus*,[8] namely, *H. cynomys* (Radford, 1941) from *Cynomys* species, *H. latiscutatus* (de Meillon & Lavoipierre, 1944) from *Rattus rattus* and *H. orcadensis* (Turk, 1946) from *Microtus orcadensis*. We are unable to distinguish morphologically the type specimens of the females of *H. latiscutatus* and *orcadensis* from our material (including specimens presented by Dr. Bregetova) of " *H. musculi* " from *Mus musculus* and *Apodemus sylvaticus* ; all occur on murines. *H. cynomys*, of which we have examined only the " type " specimen, is undoubtedly closely related to " *musculi* ", but shows differences in the form of setae av_1 and pv_1 on tarsi II and IV ; on tarsus II these setae are claw-like but longer and less distinctly curved while on tarsus IV seta av_1 is stout and spine-like and pv_1 is relatively slender and whip-like distally. In view of these slight morphological differences and the systematic position of the host (*Cynomys :* Sciuridae) we are reluctant to assign "*H. musculi* (Johnston) Bregetova" to this taxon and propose using the next available combination, *Hirstionyssus latiscutatus* (de Meillon & Lavoipierre).

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[8] *Hirstionyssus otomys* (Radford, 1942) also bears a superficial resemblance to this complex but may be readily distinguished by having only 12 setae on the palptibia and the tendency for the third pair of sternal setae to be off the sternal shield. We have recently found this species on *Arvicanthis abyssinicus* from the Congo.

KEY TO FEMALES

1 Sternal shield rectangular. Podonotal region with setae *s1* and *s2* on integument. Coxae II and III each with one spur (including anterior spur of coxa II). Palptibia with 13 seta . . . . **H. blanchardi** (Trouessart) (p. 296)

– Sternal shield arched, posterior border markedly concave. Podonotal region with setae *s1* and *s2* on shield. Coxae II and III each with two spurs. Palptibia with 12 to 14 setae 2

2 Opisthonotal region of dorsal shield with 10 or more pairs of setae. Palptibia with 14 setae 3

– Opisthonotal region of dorsal shield with eight pairs of setae. Palptibia with 12 or 13 setae 4

3 Tarsus II with setae av_1 and pv_1 stout, claw-like ; coxa IV with a small spur on its postero-distal margin. Podonotal region of dorsal shield with 16 pairs of setae (*r2* off the shield) . . . . . **H. latiscutatus** (de Meillon & Lavoipierre) (p. 291)

– Tarsus II with setae av_1 and pv_1 simple ; coxa IV without spur. Podonotal region of dorsal shield with 17 pairs of setae (*r2* off the shield) **H. isabellinus** (Oudemans) (p. 295)

4 Podonotal region with 15 pairs of setae on the dorsal shield, *s6* lacking ; three pairs of *r* setae on the cuticle . . . . **H. soricis** (Turk) (p. 286)

– Podonotal region with 16 pairs of setae on the dorsal shield, *s6* present ; four pairs of *r* setae on the cuticle 5

5 Coxa II with anterior seta short, stout and blunt ; posterior spur large and pointed. Dorsal shield with seta *z2* at least twice the length of seta *s1* **H. talpae** Zemskaya (p. 281)

– Coxa II with anterior seta simple ; posterior spur relatively smaller. Dorsal shield with setae *z2* and *s1* subequal in length **H. oryctolagi** sp. nov. (p. 286)

KEY TO MALES[9]

1 Coxa III with one spur. Palptibia with 13 setae. **H. blanchardi** (Trouessart) (p. 298)

– Coxa III with two spurs. Palptibia with 12 or 14 setae 2

2 Opisthonotal region of dorsal shield with 10 or more pairs of setae. Palptibia with 14 setae 3

– Opisthonotal region of dorsal shield with eight pairs of setae. Palptibia with 12 setae 4

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[9] Male of *H. oryctolagi* not known.

3 Coxa II with anterior spur only. Opisthogastric setae relatively short
H. isabellinus (Oudemans) (p. 296)

– Coxa II with two spurs. Opisthogastric setae extremely long
H. latiscutatus (de Meillon & Lavoipierre) (p. 291)

4 Dorsal shield with postero-lateral setae considerably longer than terminal (*Z*5) setae ; podonotal region of shield with 18 pairs of setae. Anterior seta on coxa II simple . . . . **H. talpae** Zemskaya (p. 283)

– Dorsal shield with postero-lateral and terminal (*Z*5) setae subequal in length ; podonotal region of shield with 17 pairs of setae. Anterior seta on coxa II short and stout . . . . **H. soricis** (Turk) (p. 288)

Hirstionyssus talpae Zemskaya

Liponyssus arcuatus (Koch) Oudemans, 1913, *Arch. Naturgesch. Abt.* A **79** (9) : 68, figs.
Hirstionyssus talpae Zemskaya, 1955, in Bregetova *et al.*, *Opred. Faune SSSR.* **59** : 360, figs.

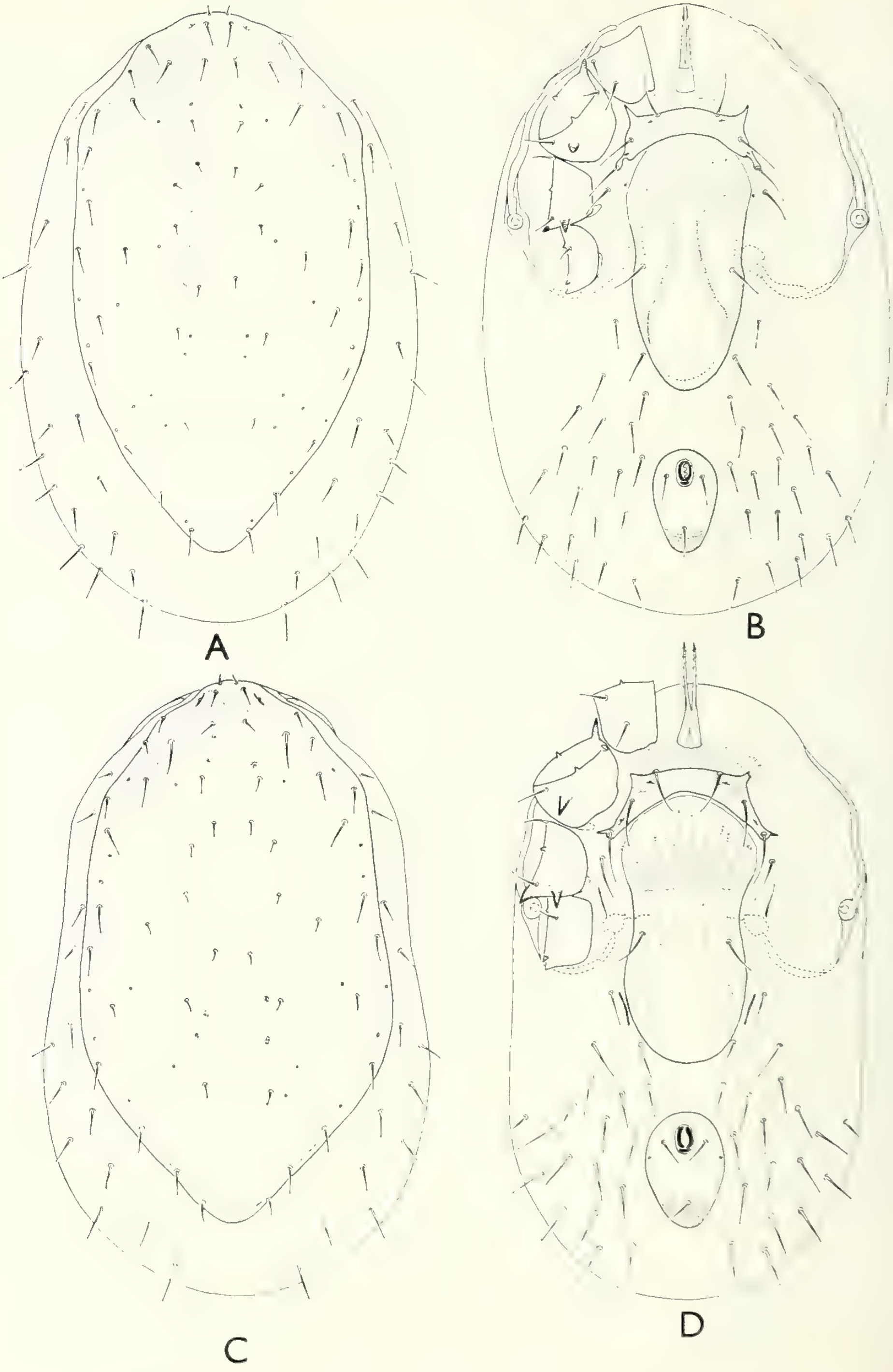
Female : Chelicera with segment I, 50 μ ; II, 93 μ ; movable digit 40 μ ; both digits edentate (Text-fig. 69C). Four pairs of gnathosomal setae with *c.s.* about 48 μ apart ; *hyp.*2 about 30 μ apart. Deutosternum with 12 rows of denticles (one to four denticles per row) . Corniculi membranous, internal malae slender, elongate ; salivary styli conspicuous (Text-fig. 68D). Tectum capituli tongue-shaped, anterior margin fimbriate (Text-fig. 69D). Pedipalp (2–5–6–12) with bi-deficient chaetotaxy on palptibia (Text-fig. 69B) ; apotele two-tined.

Dorsal shield (576 μ × 324 μ) with 24 pairs of setae distributed as in Text-fig. 67C ; seta *z*2 about twice as long as setae *s*1 and *s*2. Surface of shield granular, with reticulations anteriorly and laterally. About 13 pairs of setae on the unsclerotized integument, including *r*2, *r*3, *r*5 and *r*6 ; *r*4 is lacking.

Tritosternum with base 36 μ, laciniae 75 μ. Sternal shield (24 μ × 135 μ) arched, strongly concave posteriorly, with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 68 μ ; between *st*1 and *st*3, 80 μ. Surface of shield granular, reticulated in antero-lateral corners. Genital shield (138 μ × 114 μ) granular, with one pair of setae. Anal shield (96 μ × 78 μ) with par- and post-anal setae subequal in length (27 μ). Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 67D. Peritreme extends about to middle of coxa I ; anterior part of peritrematal shield free ; posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 stout and claw-like (Text-fig. 69F), tarsus IV with these setae long and slender (Text-fig. 69G). Anterior seta on coxa II short and stout (Text-fig. 69A). Coxal spur formula (0–2–2–1). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	60/48	60/54	45/42	60/45
tibia	60/45	48/48	42/40	54/42
tarsus	90/36	72/40	72/36	90/36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Male (large form) : Chelicera with segment I, 45 μ ; II, 84μ ; spermadactyl 45 μ long from base of movable digit (Text-fig. 69E). Four pairs of gnathosomal setae with *c.s.* about 48 μ apart, *hyp.2* about 30 μ apart. Other gnathosomal features as in female.

Dorsal shield (552 μ × 348 μ) with 26 pairs of setae distributed as in Text-fig. 68A ; *r2* and *r3* situated on the shield. Setae *z2*, *z4*, *s3*–*s6*, *r3* and postero-lateral setae considerably longer than any of the other setae. Surface of shield granular, reticulated anteriorly and laterally. Unsclerotized integument of dorsum with five pairs of setae, including *r5* and *r6*, *r4* being absent.

Tritosternum with base 33 μ, laciniae 78 μ. Holoventral shield (444 μ × 117 μ) with four pairs of setae and three pairs of pores in the sternal region, four pairs of setae in the genito-ventral region. Between *st1*, 50 μ ; between *st1* and *st3*, 98 μ. Par- and postanal setae subequal in length (30 μ). Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 68B. Peritreme extends to middle of coxa I ; fused anteriorly with dorsal shield. Posterior part of peritrematal shield very small and free.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 stout and claw-like. Stout, spine-like setae present on a number of segments : trochanter I (*d*), femur I (ad_1, pd_{1-2}) ; femur II (pd_2) ; genu and tibia II (*pv*) ; femur III (*v* and *al*) ; genu and tibia III (*av*) ; femur IV (*al* and *v*) ; genu and tibia IV (*av*) ; tarsus IV (av_1 and *mv*). All the ventral setae on tarsus III and seta *mv* on tarsus II are stout basally, tapering to long fine points. Coxa II with anterior seta relatively longer than in female. Coxal spur formula (0–2–2–1). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	60/48	70/54	57/48	75/57
tibia	60/40	50/50	50/45	70/48
tarsus	84/33	70/38	80/36	105/36

Male (small form) : A small male has been found which closely resembles the large form except in its body measurements and the relative length and thickness of the setae.

Dorsal shield (468 μ × 258 μ) with chaetotaxy as in large form. Holoventral shield (372 μ × 114 μ) a little more slender than in large form ; opisthogastric setae relatively shorter (Text-fig. 68C). Between *st1*, 50 μ ; between *st1* and *st3*, 78 μ. Par- and postanal setae about 20 μ long.

Chaetotaxy of legs as in large form, but the stout setae are not as greatly enlarged. The spur on coxa IV is a rather small, rounded process. Length/width (in μ) of leg segments :

FIG. 67. A–B. *Hirstionyssus oryctolagi* sp. nov., female ; dorsum (A) and venter (B) of idiosoma. C–D. *Hirstionyssus talpae* Zemskaya, female ; dorsum (C) and venter (D) of idiosoma.

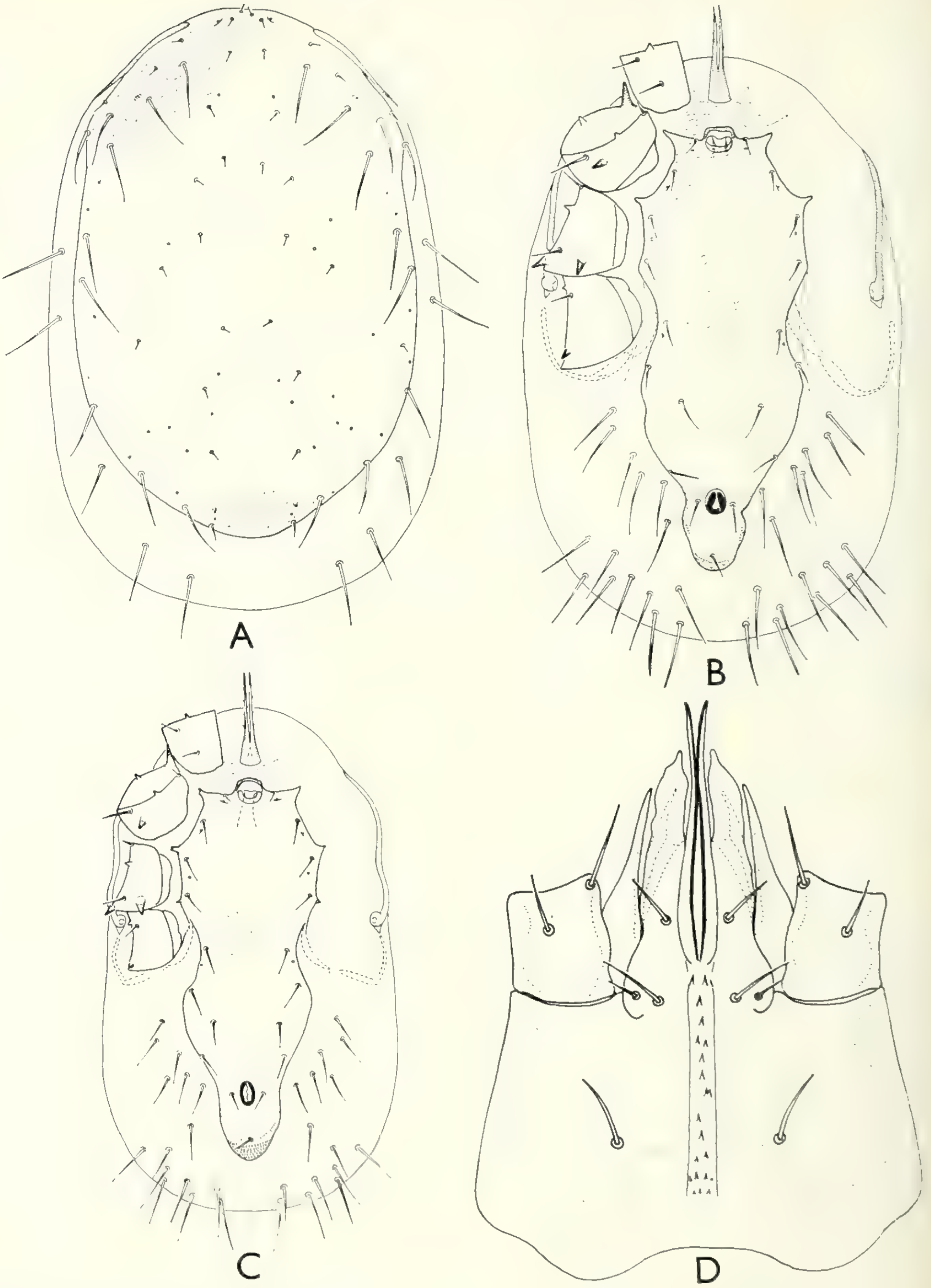


Fig. 68. *Hirstionyssus talpae* Zemskaya. A. Dorsum of idiosoma of male; B. venter of idiosoma of male, large form; C. venter of idiosoma of male, small form; D. venter of gnathosoma of female.

	I	II	III	IV
genu	52/42	54/45	40/36	50/40
tibia	50/36	42/42	36/36	48/36
tarsus	75/30	60/33	66/30	78/30

HABITAT: Common in the nests of *Talpa europaea* Linn. in Britain, Europe and the U.S.S.R.

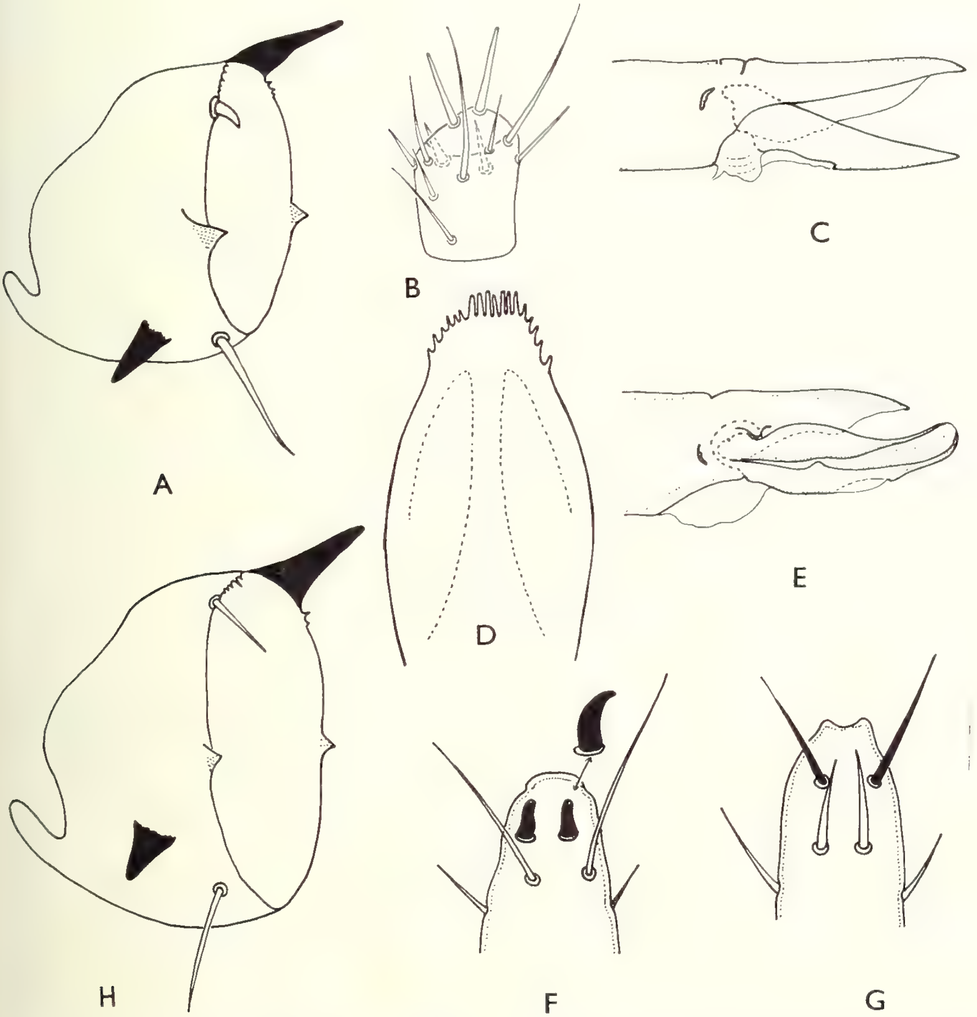


FIG. 69. A–G. *Hirstionyssus talpae* Zemskaya; coxa II of female (A); palptibia of female (B); chelicera of female (C); tectum capituli of female (D); chelicera of male (E); venter of distal third of tarsus II of female (F); venter of distal third of tarsus IV of female (G). H. *Hirstionyssus oryctolagi* sp. nov.; coxa II of female.

Hirstionyssus oryctolagi sp. nov.

Female: Chelicera with segment I, 60 μ; II, 108 μ; movable digit 50–54 μ. Four pairs of gnathosomal setae with *c.s.* about 48 μ apart, *hyp.*2 about 24–33 μ apart. Deutosternum with 14–15 rows of denticles (one to three denticles per row). Corniculi membranous; internal malae slender, elongate; salivary styli conspicuous. Tectum capituli tongue-shaped, anterior margin apparently smooth. Pedipalp (2–5–6–12/13) with uni- or bideficient chaetotaxy on palptibia; apotele two-tined.

Dorsal shield (666–672 μ × 366 μ) with 24 pairs of setae distributed as in Text-fig. 67A; setae *z*2, *z*4 and the *s* series subequal in length. Surface of shield granular with reticulations near the margin, especially anteriorly and laterally. Unsclerotized integument of dorsum with about 17 pairs of setae, including *r*2, *r*3, *r*5 and *r*6; *r*4 is absent.

Tritosternum with base 40 μ, laciniae 75 μ. Sternal shield (32 μ × 153–156 μ) with three pairs of setae and two pairs of pores; metasternals free with associated pores. Between *st*1, 75–78 μ; between *st*1 and *st*3, 84–87 μ. Surface of shield granular, reticulated in antero-lateral corners. Genital shield (150–153 μ × 123–135 μ) granular, with one pair of setae. Anal shield (102–105 μ × 75–78 μ) with paranal setae 30 μ, postanal seta 36 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 67B. Peritreme extends to middle of coxa I; posterior part of peritrematal shield fused with podal elements of coxa IV.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 stout; many leg setae robust but not greatly thickened. Coxa II with anterior seta simple (Text-fig. 69H). Coxal spur formula (0–2–2–1). Length/width (in μ) of leg segments:

	I	II	III	IV
genu	72/54	72/54	48/42	66/45
tibia	63/45	54/50	45/40	63/44
tarsus	98/36	84/40	84/36	105/38

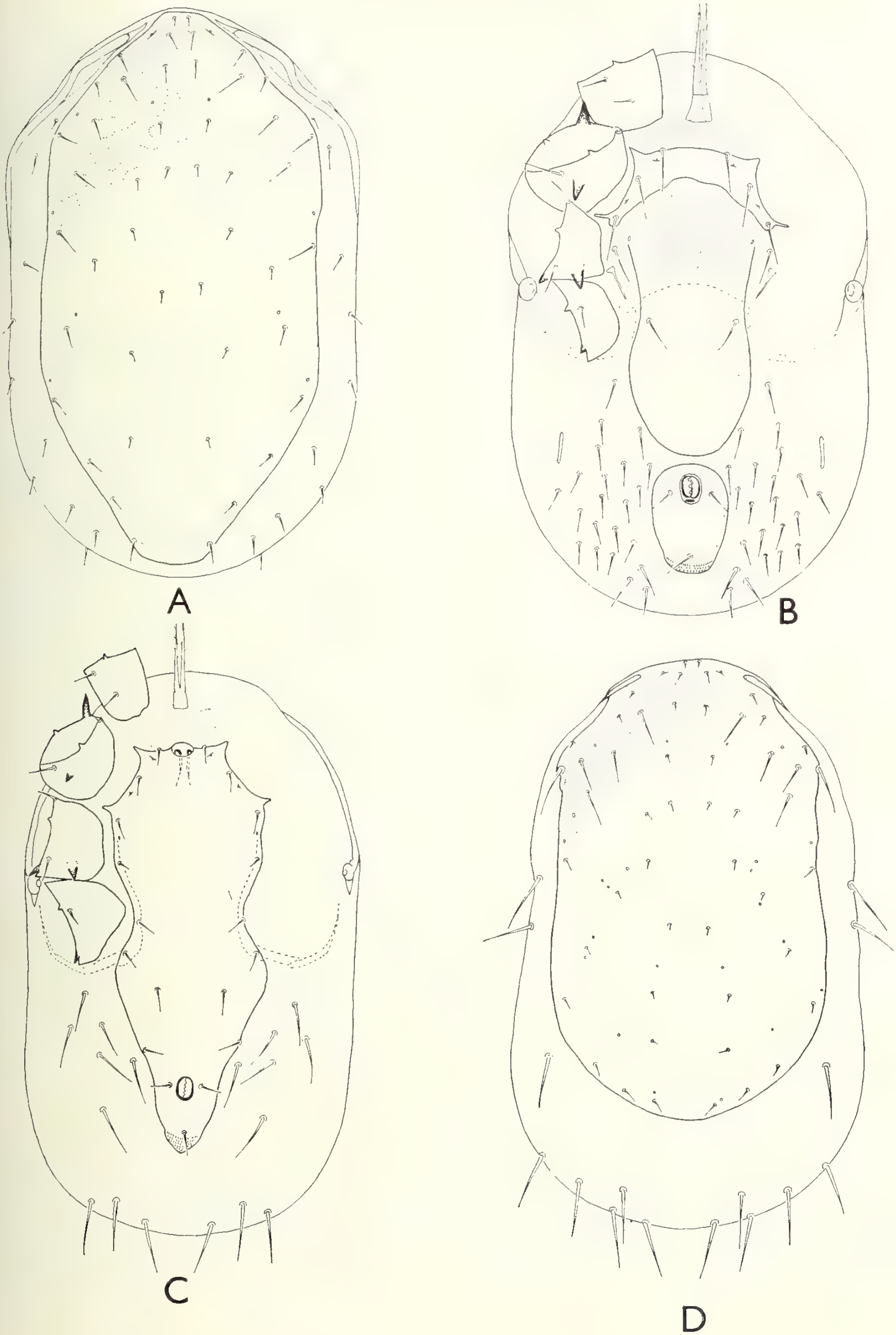
HABITAT: Found on a young rabbit, Truro, Cornwall, April, 1949 (coll. Dr. F. A. Turk). Holotype female (1965 : 12 : 29 : 30) and female paratype in the collection of the British Museum (Natural History); four female paratypes in the collection of Dr. F. A. Turk.

Hirstionyssus soricis (Turk)

Ichoronyssus soricis Turk, 1945, *Parasitology* **36** : 133, figs.
?*Hirstionyssus eusoricis* Bregetova, 1956, *Opred. Faune SSSR.* **61** : 184, figs. (nom. nov. pro. *H. soricis*: Zemskaya, 1955).

Female: Chelicera with segment I, 40 μ; II, 90 μ; movable digit 42 μ. Four

FIG. 70. *Hirstionyssus soricis* (Turk). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. venter of idiosoma of male; D. dorsum of idiosoma of male.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pairs of gnathosomal setae with *c.s.* about 40 μ apart, *hyp*.2 about 30 μ apart. Deutosternum with eleven transverse rows of denticles (one or two denticles per row). Corniculi membranous, internal malae slender, elongate ; salivary styli conspicuous. Tectum capituli tongue-shaped, anterior margin fimbriate. Pedipalp (2–5–6–12) with bideficient chaetotaxy on palptibia ; apotele two-tined.

Dorsal shield (490–504 μ × 252 μ) with 23 pairs of setae distributed as in Text-fig. 70A, seta *s*6 being absent. Surface of shield with an overall reticulate pattern, but from about the level of setae *j*3, the lines show a tendency to break up into rows of punctations. About ten pairs of setae on the unsclerotized integument, including *r*2, *r*3 and *r*5 ; *r*4 and *r*6 are lacking.

Tritosternum with base 36 μ, laciniae 66 μ. Sternal shield (30 μ × 114 μ) arched, strongly concave posteriorly, with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 60 μ ; between *st*1 and *st*3, 70–75 μ. Surface of shield with reticulations in antero-lateral corners. Genital shield (114–123 μ × 96–98 μ) with one pair of setae. Anal shield (84 μ × 70 μ) with par- and post-anal setae subequal in length (20–24 μ). Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 70B. Peritreme extends to middle of coxa I ; anterior part of peritrematal shield free, posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 stout and claw-like. Fairly stout setae on trochanter I (*d*), femur I (ad_1 and pd_{1-2}), femur II (ad_1 and pd_1), femora III and IV (ad_{1-2}). Coxa II with anterior seta short and stout. Coxal spur formula (0–2–2–1). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	54/45	54/45	38/38	48/40
tibia	50/40	42/42	36/36	48/36
tarsus	80/34	60/36	63/33	78/33

Male : Chelicera with segment I, 45 μ ; II, 80 μ ; spermadactyl 45 μ from base of movable digit. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp*.2 about 27 μ apart. Other gnathosomal features as in female.

Dorsal shield (480 μ × 276 μ) with 25 pairs of setae distributed as in Text-fig. 70D ; *r*2 and *r*3 are situated on the shield. Setae *z*2, *z*4, *s*3, *s*4 and *r*3 are considerably longer than the other setae on the shield. Marginal areas of shield reticulated, the central region being mainly granular. Unsclerotized integument with eight pairs of setae including *r*5 ; *r*4 and *r*6 are absent.

Holoventral shield (408 μ × 102 μ) with four pairs of setae and three pairs of pores in the sternal region, four pairs or setae in the genito-ventral region. Between *st*1, 48 μ ; between *st*1 and *st*3, 87 μ. Paranal setae 20 μ, postanal seta 25 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 70C. Peritreme extends to middle of coxa I, and is fused anteriorly with dorsal shield ; peritrematal shield free posteriorly.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 stout and claw-like. Several thickened dorsal setae present as in female. In addition, very stout, spine-like setae are present on the following segments : tibia II (*pv*) ; femur IV (*al* and *v*) ; genu and tibia IV (*av*) ; tarsus IV (av_1 and *mv*). Moderately stout setae are present on femur III (*al* and *v*) and genu III (*av*). Seta *mv* on tarsus II and all the ventral setae on tarsus III are thickened basally, tapering to long, fine points. Coxa II with anterior seta short and stout. Coxal spur formula (0–2–2–1). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	54/40	63/45	45/36	66/42
tibia	50/33	45/42	42/33	57/42
tarsus	70/30	57/33	75/30	84/30

Deutonymph : Chelicera with segment I, 30 μ ; II, 75 μ ; movable digit 33 μ. Four pairs of gnathosomal setae with *c.s.* about 36 μ apart, *hyp.*2 about 24 μ apart. Deutosternum with ten rows of denticles (one to two denticles per row). Tectum capituli with anterior margin smooth. Other gnathosomal features as in female.

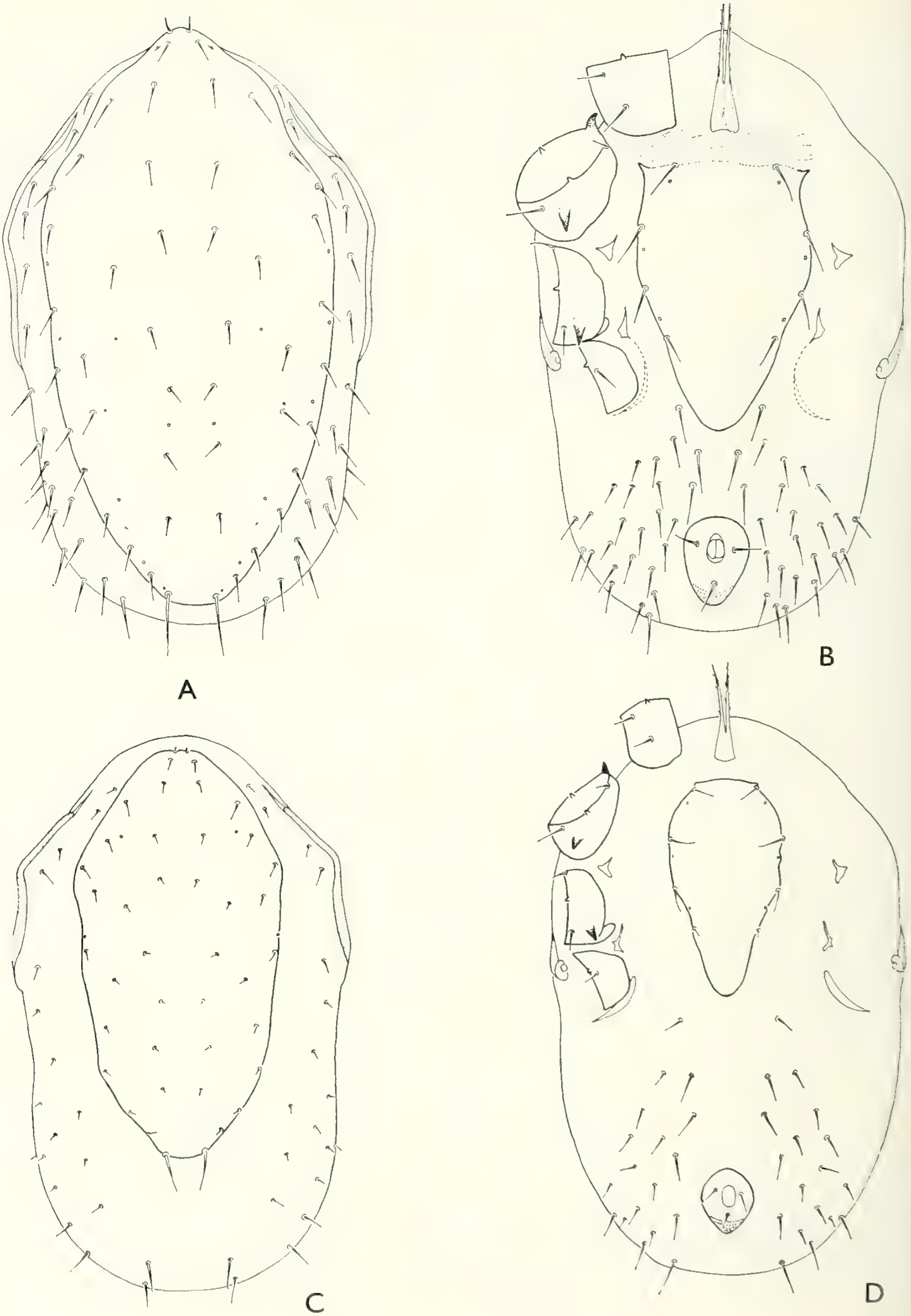
Dorsal shield (336 μ × 144–162 μ) with 21 pairs of setae distributed as in Text-fig. 71C ; *s*1 and *s*2 are off the shield. Terminal setae (*Z*5) more than twice as long as the other setae on the shield. Surface of shield reticulated, the " lines " consisting of rows of punctations. Unsclerotized integument of dorsum with about 19 pairs of setae, including *s*1, *s*2, *r*2, *r*3 and *r*6.

Tritosternum with base 27 μ, laciniae 54 μ. Sternal shield (153–168 μ × 93–98 μ) with four pairs of setae and three pairs of pores ; metasternal setae shorter than the sternals. Between *st*1, 48 μ ; between *st*1 and *st*3, 81–84 μ. One pair of genital setae situated lateral or postero-lateral to posterior tip of shield. Anal shield (40 μ × 40 μ) with paranal setae 15–18 μ long, postanal seta 15 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 71D. Peritreme extends nearly to anterior margin of coxa II. Anterior part of peritrematal shield free, posterior part not developed.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 simple. Coxal spur formula (0–2–1–0). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	42/42	42/42	36/34	36/33
tibia	42/38	40/40	33/30	38/33
tarsus	63/32	60/30	68/27	75/27

HABITAT : Found on *Sorex minutus* Linn., Camborne, Cornwall (type material from collection of Dr. F. A. Turk) ; *Sorex araneus* Linn., Craighouse, Jura, Inner Hebrides (coll. Dr. G. B. Corbet, 6th July, 1961), and a shrew, West Horsley, Surrey (coll. Dr. M. Burton, 22nd August, 1957).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Hirstionyssus latiscutatus (de Meillon & Lavoipierre)

Liponyssus latiscutatus de Meillon & Lavoipierre, 1944, *J. ent. Soc. S. Afr.* **7** : 62.
Ichoronyssus orcadensis Turk, 1946, *Ann. Mag. nat. Hist.* (11) **12** : 786, figs. 1–7. (**syn. nov.**).
Hirstionyssus musculi (Johnston) Bregetova, 1956, *Opred. Faune* SSSR. **61** : 185, figs.

Female : Chelicera with segment I, 60 μ ; II, 114 μ ; movable digit 50 μ. Four pairs of gnathosomal setae with *c.s.* about 54 μ apart, *hyp.*2 about 33 μ apart. Deutosternum with about 14 rows of denticles (one to three denticles per row). Corniculi membranous, internal malae slender. Tectum capituli tongue-shaped, anterior margin rounded, fringed. Salivary styli conspicuous. Pedipalp (2–5–6–14) with normal chaetotaxy (Text-fig. 72C) ; apotele two-tined.

Dorsal shield (552 μ × 294 μ) with 26 or more pairs of setae distributed as in Text-fig. 72A. The setae on the opisthonotal region are variable in number and distribution. There may, for example, be one or two setae between the first and second pairs of *J* setae. Surface of shield granular, with reticulations near the antero-lateral margins ; unsclerotized integument of dorsum with about 19 pairs of setae, including five pairs of *r* setae.

Tritosternum with base 45 μ, laciniae 78 μ. Sternal shield (27 μ × 144 μ) arched, posterior margin deeply concave ; with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Surface of shield granular with reticulations in the antero-lateral corners. Between *st*1, 70 μ ; between *st*1 and *st*3, 72 μ. Genital shield (108 μ × 108 μ) tongue-shaped, granular, with one pair of setae. Anal shield (84 μ × 72 μ) with paranal setae 30 μ, postanal setae 36 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 72B. Peritreme extends to middle of coxa I ; peritrematal shield fused posteriorly with podal elements of coxa IV.

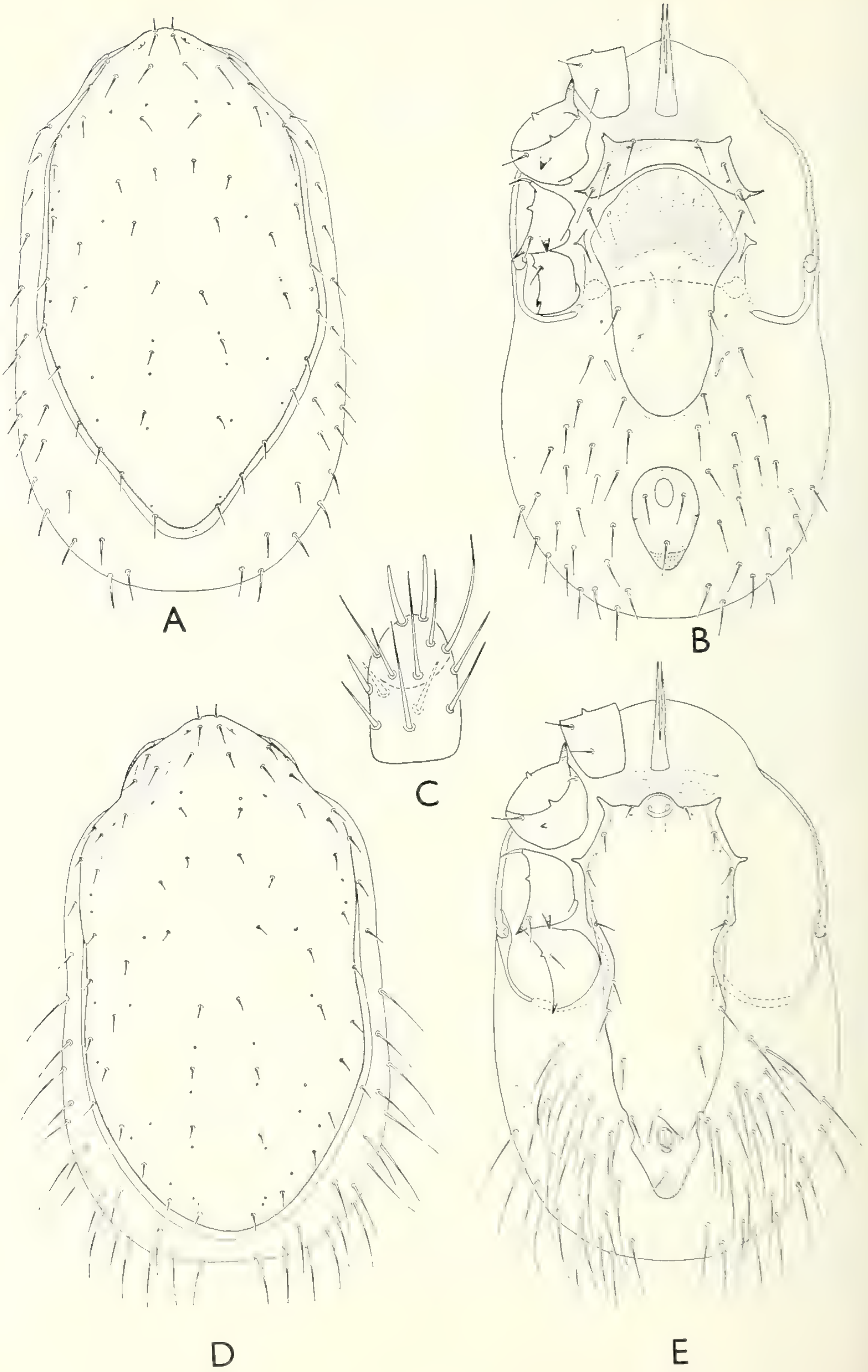
Chaetotaxy of legs normal ; tarsus II with setae av_1 and pv_1 stout and claw-like. Coxal spur formula (0–2–2–1). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	63/48	63/48	45/38	63/38
tibia	63/42	50/45	45/36	60/36
tarsus	96/36	78/36	90/30	110/32

Male : Chelicera with segment I, 45 μ ; II, 90 μ ; spermadactyl 42 μ long from base of movable digit. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp.*2 about 30 μ apart. Other features as in female.

Dorsal shield (468 μ × 294 μ) with 28 or more pairs of setae distributed as in Text-fig. 72D ; unsclerotized integument of dorsum with 19 pairs of setae including three pairs of *r* setae. Surface of shield granular with reticulations antero-laterally.

FIG. 71. A–B. *Hirstionyssus latiscutatus* (de Meillon and Lavoipierre), deutonymph ; dorsum (A) and venter (B) of idiosoma. C–D. *Hirstionyssus soricis* (Turk), deutonymph ; dorsum (C) and venter (D) of idiosoma.


A
B
C
D
E

Tritosternum with base 33 μ, laciniae 72 μ. Holoventral shield (360 μ × 117 μ) with four pairs of setae and three pairs of pores in the sternal region, four pairs of setae in the genito-ventral region. Between *st*1, 50 μ; between *st*1 and *st*3, 72 μ. Paranal setae 33 μ, postanal seta 27 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 72E. Peritreme extends to middle of coxa I; peritrematal shield fused anteriorly with dorsal shield, posteriorly with podal elements of coxa IV.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 stout and claw-like. Stout, spine-like setae present on genu IV (*av*), tibia IV (*av*) and tarsus IV (av_1 and *mv*). Coxal spur formula (0–2–2–1). Length/width (in μ) of leg segments:

	I	II	III	IV
genu	60/40	60/42	50/38	66/40
tibia	54/36	45/42	45/36	63/36
tarsus	80/30	66/30	75/30	100/30

Deutonymph: Chelicera with segment I, 45 μ; II, 72 μ; movable digit 40 μ. Four pairs of gnathosomal setae with *c.s.* about 40 μ apart, *hyp*.2 about 26 μ apart. Tectum capituli with anterior margin weakly denticulate. Other gnathosomal features as in female.

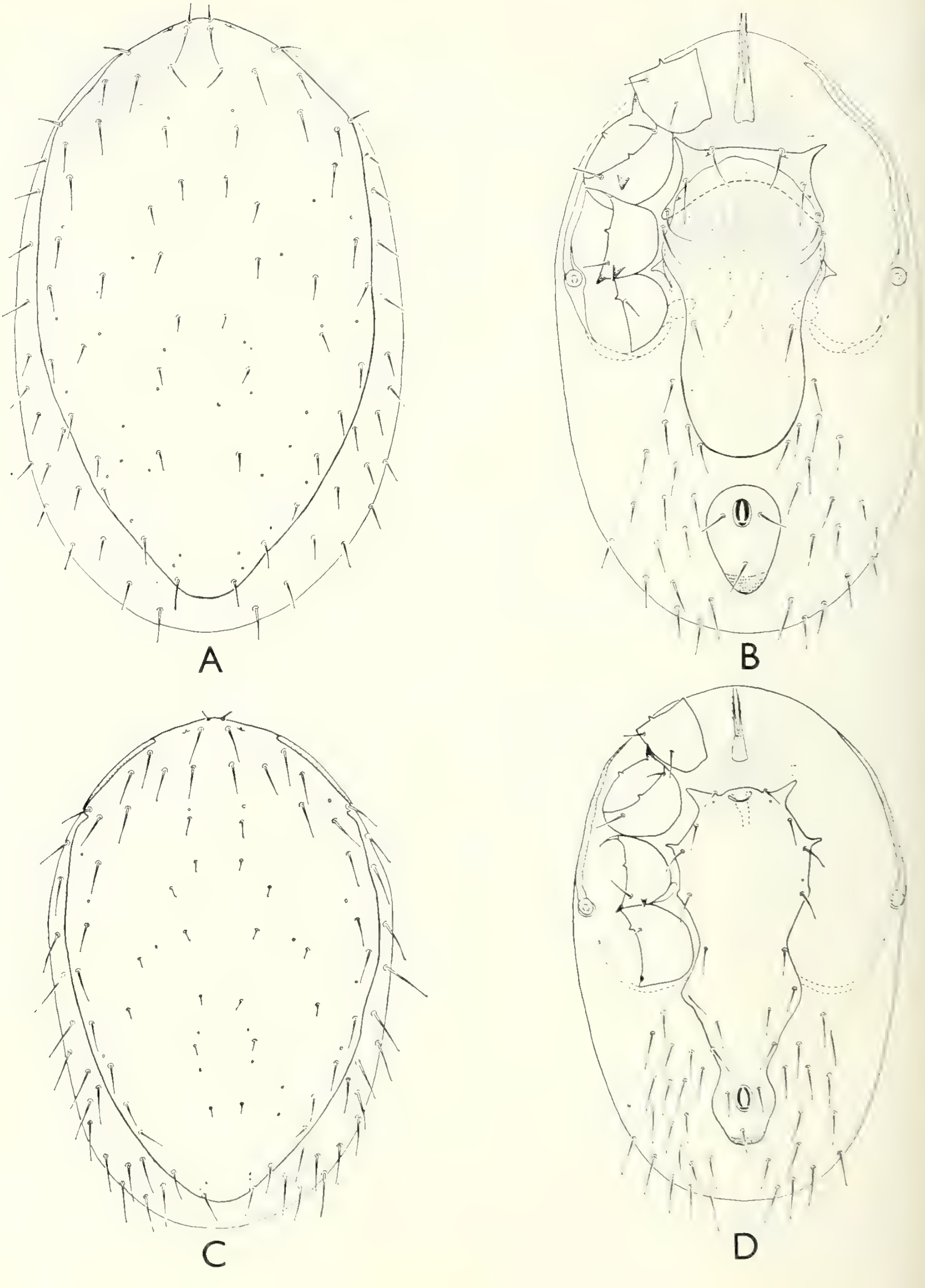
Dorsal shield (372 μ × 180 μ) with 24 pairs of setae distributed as in Text-fig. 71A; unsclerotized integument with about 20 pairs of setae, including *s*1, *s*2 and five pairs of *r* setae.

Tritosternum with base 30 μ, laciniae 50 μ. Sternal shield (180 μ × 114 μ) with four pairs of setae (sternal and metasternal) and three pairs of pores. One pair of genital setae is situated on the integument lateral to the posterior tip of the shield. Between *st*1, 66 μ; between *st*1 and *st*3, 84 μ. Anal shield (45 × 45 μ); par- and postanal setae subequal in length (about 20 μ). Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 71B. Peritreme extends to anterior fourth of coxa II; anterior part of peritrematal shield extends to posterior fourth of coxa I, posterior part not developed.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 simple. Coxal spur formula (0–2–1–0). Length/width (in μ) of leg segments:

	I	II	III	IV
genu	50/42	48/42	34/36	45/36
tibia	48/38	42/40	36/34	45/33
tarsus	75/32	60/30	70/27	80/30

FIG. 72. *Hirstionyssus latiscutatus* (de Meillon & Lavoipierre). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. palptibia of female; D. dorsum of idiosoma of male; E. venter of idiosoma of male.


A
B
C
D

HABITAT : Found in Britain on *Microtus orcadensis* Millais, Scotland, and on laboratory mice, Newcastle-upon-Tyne. Also recorded from South Africa (on *Rattus rattus* (Linn.) and the U.S.S.R. (on *Rattus* species, *Mus musculus* Linn., *Apodemus* species, *Micromys minutus* (Pallas), *Microtus* species).

Hirstionyssus isabellinus (Oudemans)

?*Liponyssus albato-affinis* Oudemans, 1903, *Tijdschr. Ned. dierk. Vereen.* (2) **8** : 24.
Liponyssus isabellinus Oudemans, 1913, *Ent. Ber. Amst.* **3** : 384, et *Arch. Naturgesch. Abt. A* **79** (9) : 80, figs.
Hirstionyssus isabellinus : Bregetova, 1956, *Opred. Faune SSSR.* **61** : 181, figs.
Hirstionyssus arvicolae Zemskaya, 1955, in Bregetova *et al.*, *Opred. Faune SSSR.* **59** : 366, figs. 790–792.

Female : Chelicera with segment I, 66 μ ; II, 135 μ ; movable digit 57 μ. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 40 μ apart. Deutosternum with 13 rows of denticles (one or two denticles per row). Corniculi membranous, internal malae long and slender. Tectum capituli tongue-shaped, anterior margin fimbriate. Salivary styli conspicuous. Pedipalp (2–5–6–14) with two-tined apotele.

Dorsal shield (558 μ × 324 μ) with 27 pairs of setae distributed as in Text-fig. 73A, seta *r*2 being on the shield. Surface of shield granular with reticulations antero-laterally. Unsclerotized integument with about 16 pairs of setae, including four pairs of *r* setae (*r*3–*r*6).

Tritosternum with base 42 μ, laciniae 84 μ. Sternal shield (42 μ × 158 μ) arched, strongly concave posteriorly, with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 84 μ ; between *st*1 and *st*3, 90 μ. Surface of shield granular with reticulations antero-laterally. Genital shield (156 μ × 138 μ) granular, with one pair of setae. Anal shield (96 μ × 87 μ) with paranal setae 33 μ, postanal seta 36 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 73B. Peritreme extends to anterior third of coxa I ; anterior part of peritrematal shield free, posterior part fused with podal shields of coxa IV.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 simple. Coxal spur formula (0–2–2–0). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	66/45	66/45	45/36	63/36
tibia	66/40	50/45	42/36	60/36
tarsus	99/33	75/34	80/30	114/30

FIG. 73. *Hirstionyssus isabellinus* (Oudemans). A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. dorsum of idiosoma of male ; D. venter of idiosoma of male.

Male : Chelicera with segment I, 48 μ ; II, 87 μ ; spermadactyl 50 μ. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.*2 about 30 μ apart. Other gnathosomal features as in female.

Dorsal shield (508 μ × 312 μ) with 27 pairs of setae distributed as in Text-fig. 73C ; unsclerotized integument of dorsum with 16 pairs of setae, including *r*3–*r*6.

Holoventral shield (360 μ × 108 μ) with four pairs of setae in the sternal region and four pairs in the genito-ventral region. Between *st*1, 50 μ ; between *st*1 and *st*3, 74 μ. Par- and postanal setae about 27 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 73D. Peritreme extends to anterior fourth of coxa I and is fused anteriorly with the dorsal shield; posterior part of peritrematal shield weakly developed.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 stout and claw-like. Coxal spur formula (0–1–2–1). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	66/42	66/45	50/40	78/45
tibia	60/36	48/42	48/36	78/40
tarsus	90/30	80/32	78/30	120/33

HABITAT : Found in Britain on the weasel (*Mustela* sp.), Brentwood, Essex ; on *Sorex araneus* Linn., Meall Greigh, Perthshire, and on *Microtus agrestis* (Linn.), Isle of Muck, Hebrides. Recorded by Oudemans from *Putorius* sp., *Arvicola terrestris* (Linn.) and *Mus musculus* Linn. in Holland, and by Bregetova from *Mustela nivalis* Linn., *Rattus norvegicus* (Berkenhout), *Microtus arvalis* (Pallas) and other rodents in the U.S.S.R.

The above description of the female is based on a specimen from *Mustela* sp. and that of the male on a specimen from *Microtus arvalis* presented by Dr. N. G. Bregetova. The male we have described differs from the male attributed to the species by Oudemans (1913, fig. 302) in lacking a ventral spur on coxa II. Oudemans lists a variety of hosts for this species and it is possible that his male and female are not conspecific.

Hirstionyssus blanchardi (Trouessart)

Leiognathus blanchardi Trouessart, 1904, *Arch. Parasitol. Paris* **8** : 558.
Liponyssus blanchardi: Hirst, 1922, *Proc. zool. Soc. Lond* (1921) : 787, figs.
Hirstionyssus blanchardi: Bregetova, 1956, *Opred. Faune SSSR.* **61** : 177.

Female : Chelicerae with segment I, 78 μ ; II, 138 μ ; movable digit 60 μ. Four pairs of gnathosomal setae with *c.s.* about 57 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with 18 rows of denticles (one or two denticles per row). Corniculi membranous, internal malae slender. Tectum capituli tongue-shaped, somewhat pointed anteriorly, margin smooth. Salivary styli conspicuous. Pedipalp (2–5–6–13) with unideficient chaetotaxy on palptibia (Text-fig. 74B) ; apotele two-tined.

Dorsal shield (660 μ × 324 μ) with 24 pairs of setae distributed as in Text-fig. 74A. Unsclerotized integument of dorsum with about 25 pairs of setae, including *s*1, *s*2

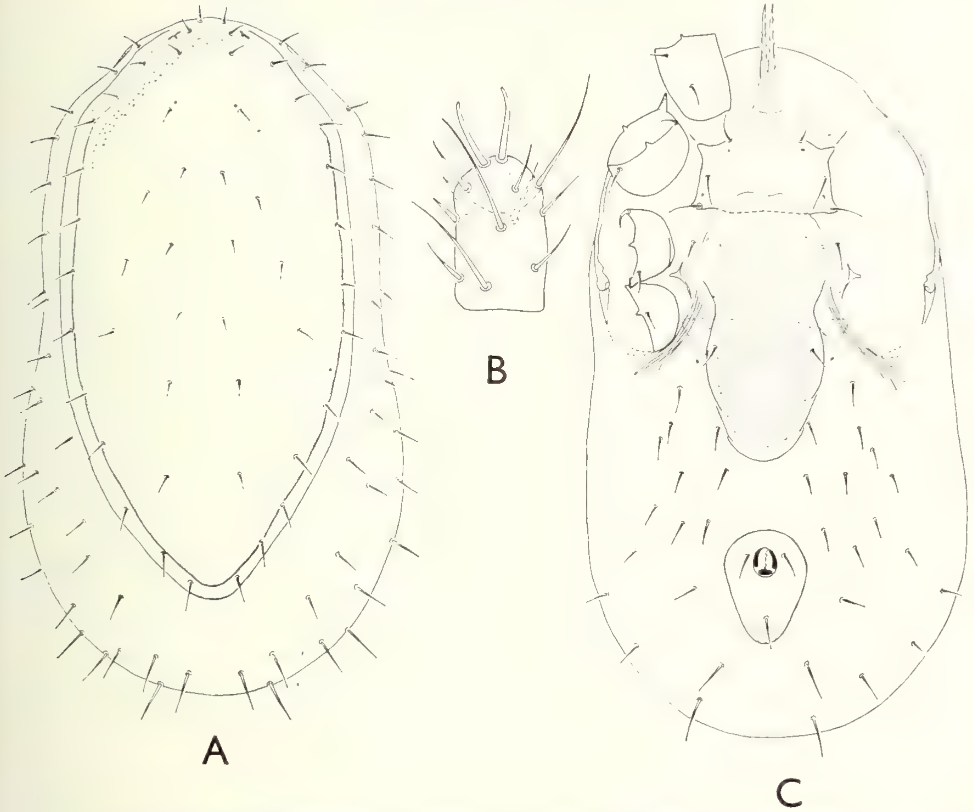


FIG. 74. *Hirstionyssus blanchardi* (Trouessart), female ; dorsum of idiosoma (A) ; palp-tibia (B) ; venter of idiosoma (C).

and six pairs of *r* setae. Surface of shield granular, with a less heavily sclerotized marginal band.

Tritosternum with base 45 μ, laciniae about 75 μ. Sternal shield (87 μ × 141 μ) rectangular, with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 80 μ ; between *st*1 and *st*3, 84 μ. Genital shield (132 μ × 132 μ) granular except for the weakly sclerotized marginal zone, bearing one pair of setae. Anal shield (99 μ × 96 μ) with paranal setae 30 μ, postanal seta 33 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 74C. Peritreme extends to middle of coxa I ; peritrematal shield fused posteriorly with podal elements of coxa IV.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 simple. Coxal spur formula (0–1–1–0). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	84/48	84/50	66/42	90/42
tibia	80/40	—	60/40	80/40
tarsus	100/36	—	100/33	126/36

Male: Chelicera with segment I, 72 μ; II, 117 μ; spermadactyl 54 μ. Four pairs of gnathosomal setae with *c.s.* 45–52 μ apart; *hyp.*2 30–36 μ apart. Deutosternum with about 15 rows of denticles (one to two denticles per row). Other features as in female.

Dorsal shield (580–615 μ × 324 μ) with 26 pairs of setae distributed as in Text-fig. 75A; fifteen pairs of setae on the unsclerotized integument, including six pairs of *r* setae. Surface of shield as in female.

Tritosternum with base 30 μ, laciniae 72 μ. Holoventral shield (444 μ × 120–138 μ) with four pairs of setae and three pairs of pores in the sternal region, four pairs of setae in the genito-ventral region. Between *st*1, 60–70 μ; between *st*1 and *st*3, 87–98 μ. Surface of shield granular. Par- and post-anal setae subequal in length (about 30 μ). Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 75B. Peritreme extends to middle of coxa I; peritrematal shields free posteriorly.

Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 stout and claw-like Stout spine-like setae on trochanter I (*d*), femora I and II (ad_1 and pd_{1-2}), femur III (*al* and *v*). Coxal spur formula (0–1–1–1). Legs bent, not suitable for measurement.

Deutonymph: Chelicera with segment I, 38 μ; II, 96 μ; movable digit 40 μ. Four pairs of gnathosomal setae with *c.s.* about 36–45 μ apart, *hyp.*2 about 26–30 μ apart. Deutosternum with 13–16 rows of denticles (one or two denticles per row). Other features as in female.

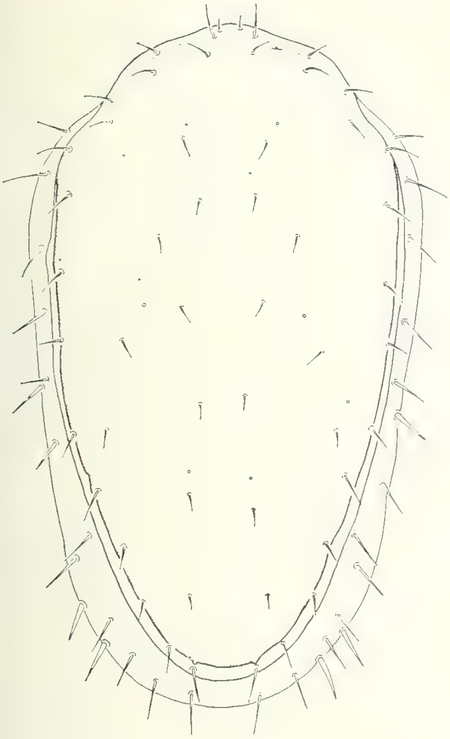
Dorsal shield (408–444 μ × 156–210 μ) with 24 pairs of setae distributed as in Text-fig. 75C; about 20 pairs of setae on the unsclerotized integument, including *s*1, *s*2 and six pairs of *r* setae.

Tritosternum with base 30 μ, laciniae 57 μ. Sternal shield (240–252 μ × 110–120 μ) with four pairs of setae and three pairs of pores; one pair of genital setae is situated on the cuticle lateral to the posterior tip of the shield. Between *st*1, 70–72 μ; between *st*1 and *st*3, 100–108 μ. Anal shield (48–54 μ × 50–57 μ) with par- and postanal setae subequal in length (about 15 μ). Chaetotaxy and sclerotization of venter as in Text-fig. 75D. Peritreme extends to a point between coxae I and II; anterior part of peritrematal shield short, posterior part not developed.

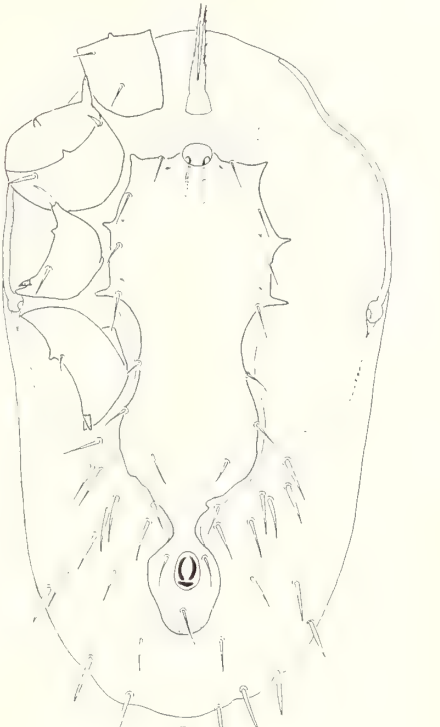
Chaetotaxy of legs normal. Tarsus II with setae av_1 and pv_1 simple. Slightly thickened setae present on femora I (ad_1 and pd_{1-2}) and II (*ad*). Coxal spur formula (0–1–0–0). Length/width (in μ) of leg segments:

	I	II	III	IV
genu	48/40	45/42	36/36	50/38
tibia	54/36	42/38	36/34	54/36
tarsus	75/30	—	60/27	93/27

FIG. 75. *Hirstionyssus blanchardi* (Trouessart). A. Dorsum of idiosoma of male; B. venter of idiosoma of male; C. dorsum of idiosoma of deutonymph; D. venter of idiosoma of deutonymph.



A



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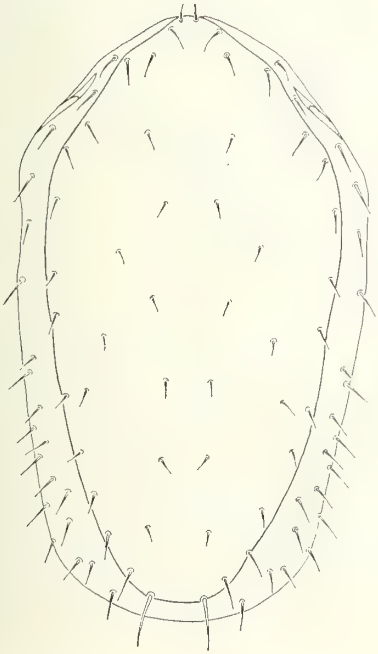

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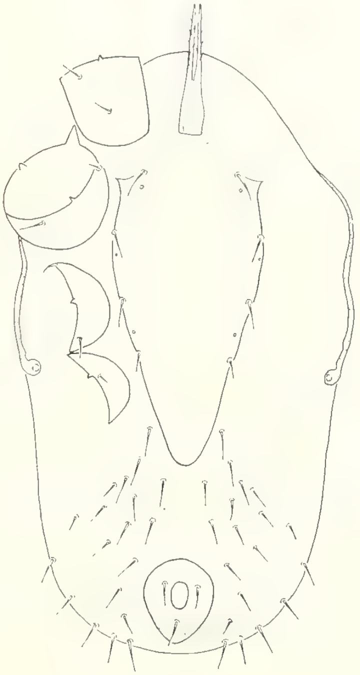

D

HABITAT: Found on *Marmota marmota* (Linn.), the Alpine Marmot, Zermatt, Switzerland, and on *Cynomys ludovicianus* (Ord.) the Black-tailed Prairie Dog (specimens kept in captivity), Horsham, England.

Subfamily **MACRONYSSINAE** Oudemans

Liponyssinae Ewing, 1923, *Proc. U.S. nat. Mus.* **62** (art. 13) : 2. [see p. 240]
Macronyssidae Oudemans, 1936, *Kritisch Historisch Overzicht der Acarologie* (III) A : 430.

Adults: Chelicerae essentially chelate-edentate, digits often with membranous lobes and denticulate processes; spermadactyl relatively short and free, rarely long and entirely fused with the movable digit; fixed digit rarely shorter than the movable. Pilus dentilis absent, dorsal seta minute or absent; fissures normal; arthrodial processes rarely present. Chaetotaxy of venter of gnathosoma normal. Pedipalps with five free segments, apotele two-tined, rarely simple; chaetotaxy of trochanter to tibia normal (2–5–6–14) or with tibia unideficient, rarely femur and and genu unideficient or tibia bideficient. Palptrochanter usually with medioventral keel in female. Deutosternum with denticles in a single file, rarely with two to five denticles in a transverse row. Hypostome somewhat elongated, corniculi membranous, internal malae free or fused. Tectum capituli elongated with margins smooth, weakly denticulated or fimbriated.

Dorsal sclerotization reduced in the female, comprising an entire shield, two subequal shields or a podonotal shield, mesonotal scutellae and a small pygidial shield; male with entire dorsal shield. Primary chaetotaxy of the dorsum of the idiosoma showing hypotrichy, paravertical setae (*z*1) normally absent. Secondary hypertrichy of the dorsum common, particularly of the lateral and marginal series. Dorsal setae simple, pilose or subspinose.

Tritosternum bipartite, laciniae smooth or pilose and often with denticulate, hyaline, lateral margins. Sternal shield in female with two or three pairs of setae and two pairs of pores; metasternal setae free, rarely absent. "Porose areas" present in the region of the first pair of sternal pores or posterior margin of sternal shield with a strongly sclerotized band in some chiropteran parasites. Genital shield usually tapering posteriorly and bearing the genital setae (except in *Ophionyssus*): opisthogastric setae may be present on the shield. Anal shield normal, aciculated area conspicuous, no euanal setae. Opisthogastric cuticle invariably hypertrichous. Metapodal shields small, relatively inconspicuous. Peritrematal shield fused with podal shields posterior to coxae IV; peritemes of varying lengths. Podal shields weakly developed. Male with holoventral shield; sternito-genital and ventro-anal shields; sternito-genital, ventral and ventro-anal shields; sternito-genital, ventral and anal shields; or sternito-genital and anal shields. Genital orifice presternal.

All legs six-segmented and with well developed ambulacra. Segmental chaetotaxy extremely diverse, never entirely normal. Coxae II–IV may have sclerotized ridges of varying degrees of development. Anterior spine of coxa II usually large, rarely minute or absent.

Larva : Inactive non-feeding instar. Chelicerae with digits minute, edentate and lacking setae, fissures and arthrodial processes. Pedipalps five-segmented ; chaetotaxy of tibia and tarsus deficient. Hypostome with two pairs of setae, corniculi degenerate, deutosternal denticles weak or absent. Idiosoma without distinct sclerotization. Podonotal region with eight or nine pairs of setae, opisthonotal region with three pairs of relatively long setae. Tritosternum bipartite but laciniae strongly reduced. Sternal region with normal three pairs of setae, opisthogastric region with two pairs, normal three setae associated with the non-functional anus. Stigmata and peritremes absent. Leg chaetotaxy normal for this instar. The larval stage is known only for a few species (*Ornithonyssus*, *Macronyssus* and *Ophionyssus*)

Protonymph : Active feeding instar. Chelicerae, basis capituli and hypostome with the characteristics of the female. Pedipalpal chaetotaxy normal (1–4–5–12), palptrochanter rarely with medio-ventral keel.

Dorsal sclerotization comprising well developed podonotal, mesonotal and pygidial elements. Podonotal shield usually with 10 or 11 pairs of setae, pygidial shield with two to seven pairs, hypertrichy of lateral and marginal series of setae of the opisthonotum common. Tritosternum as in female. Sternal shield with three pairs of setae and two pairs of pores, genital setae present, anal shield normal. Opisthogastric cuticle usually with four pairs of setae, hypertrichy of opisthogaster rare. Stigmata and short peritremes present. Chaetotaxy of legs normal for this instar except on genu IV ($2\text{—}\frac{2}{0}, \frac{2}{0}\text{—}1$) in *Ophionyssus.*

Deutonymph : Inactive, non-feeding instar characteristic of the macronyssines. Chelicerae degenerate, digits minute, hypostome with discrete corniculi and internal malae, deutosternal denticles as in female, gnathosomal setae normal. Pedipalps (2–5–6–12/13). Idiosoma without distinct sclerotization. Sexual dimorphism apparent in the dorsal and opisthogastric chaetotaxy, the male and female deutonymphs having similar chaetotaxy to the adult male and female respectively. Tritosternum simple, bipartite only at its tip. Intercoxal region with four (metasternals absent) or five pairs of setae. Stigmata, peritremes and segmental chaetotaxy of the legs as in the adult.

KEY TO THE GENERA OF THE BRITISH MACRONYSSINAE

FEMALES

1 Dorsum of the idiosoma partially covered by discrete, subequal, podonotal and opisthonotal shields . . . . **STEATONYSSUS** (p. 329)

– Dorsum of the idiosoma with an entire shield or, if with two or more scutal elements, the pygidial shield is relatively minute 2

2 Genu and tibia III each with one postero-lateral seta (genu $2\text{—}\frac{2}{1}, \frac{2}{1}\text{—}1$; tibia $2\text{—}\frac{1}{1}, \frac{2}{1}\text{—}1$) ; tritosternum without hyaline denticulate border ; " porose " areas present in region of first pair of sternal pores ; fixed digit of chelicera with distal acuminate lobe and retrose denticular processes, movable digit with dorsal hyaline flap usually with denticular processes ; sclerotized ridges of varying degrees of development usually present on ventral surfaces of coxae II–IV **MACRONYSSUS** (p. 303)

– Genu and tibia III each with two postero-lateral setae (genu $2—\frac{2}{1}, \frac{2}{1}—2$; tibia $2—\frac{1}{1}, \frac{2}{1}—2$) ; tritosternum with hyaline denticulate border ; "porose" areas absent on sternal shield ; cheliceral digits with membranous lobes but usually lacking denticular processes ; without sclerotized ridges on coxae II–IV . 3

3 Genu IV with two postero-lateral setae ($2—\frac{2}{1}, \frac{2}{1}—2$ or $2—\frac{2}{1}, \frac{3}{1}—2$) ; genital setae on integument ; ectoparasites of reptiles . . . ***OPHIONYSSUS*** (p. 335)

– Genu IV with one postero-lateral seta ($2—\frac{2}{1}, \frac{3}{1}—1$) ; genital setae situated on the genital shield ; ectoparasites of birds and mammals ***ORNITHONYSSUS*** (p. 313)

MALES

1 Ventral sclerotization comprising discrete sternito-genital and anal shields ; genu IV with two posterolateral setae ($2–\frac{2}{1},\frac{2}{1}–2$ or $2–\frac{2}{1},\frac{3}{1}–2$) . . . . . ***OPHIONYSSUS***

– Ventral sclerotization comprising holoventral shield, sternito-genital and ventro-anal shields or sternito-genital, ventral and ventro-anal shields, never with discrete anal shield ; genu IV with one postero-lateral seta ($2–\frac{2}{1}–\frac{3}{1}–1$) 2

2 Genu and tibia III each with one postero-lateral seta, segments respectively with nine and eight setae ; tritosternum with a hyaline denticulate border . . ***MACRONYSSUS***

– Genu and tibia III each with two postero-lateral setae, segments respectively with ten and nine setae ; tritosternum with a hyaline denticulate border . . 3

3 Movable digit of chelicera with a membranous lobe between the spermadactyl and the digit ; ectoparasites of Chiroptera . . . . ***STEATONYSSUS***

– Movable digit without membranous lobe between the spermadactyl and the digit ; ectoparasites of birds and mammals . . . . ***ORNITHONYSSUS***

KEY TO THE PROTONYMPHS OF THE BRITISH MACRONYSSINAE

1 Genu IV with six setae ($1—\frac{2}{0}, \frac{2}{0}—1$) 2

– Genu IV with five setae ($1—\frac{2}{0}, \frac{2}{0}—0$) 3

2 Pygidial shield with three pairs of setae (Text-fig. 92A) ***Ophionyssus natricis*** (Gervais) (p. 340)

– Pygidial shield with two pairs of setae (Text-fig. 92C) ***Ophionyssus saurarum*** (Oudemans) (p. 344)

3 Podonotal seta *j*3 and opisthonotal seta *J*5 absent (Text-fig. 84A) 4

– Podonotal seta *j*3 and opisthonotal seta *J*5 present (Text-fig. 88A) 5

4 Pygidial shield with four pairs of setae ; podonotal setae *j*5 about equal in length to the distance between the bases of setae *j*5 and *z*5 ***Ornithonyssus bacoti*** (Hirst) (p. 324)

– Pygidial shield with three pairs of setae ; podonotal setae *j*5 less than one half the length of the distance between the bases of setae *j*5 and *z*5 ***Ornithonyssus sylviarum*** (Canestrini & Fanzago) (p. 321)

5 Pygidial shield with four pairs of setae (Text-fig. 88A) 6

– Pygidial shield with five to seven pairs of setae 7

6 Pygidial shield with setae *Z*4, *S*5 and *Z*5 subequal ***Steatonyssus periblepharus*** Kolenati (p. 333)

– Pygidial shield with setae *Z*4, *S*5 and *Z*5 increasing in size in that order ***Steatonyssus occidentalis*** (Ewing)

7 Pygidial shield with seven pairs of setae 8

– Pygidial shield with five or six pairs of setae 9

8 Unsclerotized integument of idiosoma with 16 pairs of setae (excluding *j*1), Text-fig. 79A–B. . . . . . **Macronyssus kolenatii** (Oudemans) (p. 314)

– Unslcerotized integument of idiosoma markedly hypertrichous (Text-fig. 79C–D) **Macronyssus flavus** (Kolenati) (p. 310)

9 Pygidial shield with five pairs of setae **Macronyssus ellipticus** (Kolenati) (p. 307)

– Pygidial shield with six pairs of setae 10

10 Tritosternum with denticulate, hyaline border. Pygidial shield truncated or slightly concave anteriorly ; its width at least twice its length ; setae *J*4 situated on the anterior margin of the shield . **Ornithonyssus pipistrelli** (Oudemans) (p. 329)

— Tritosternum without denticulate, hyaline border. Pygidial shield convex anteriorly ; its width not more than $1\frac{1}{2}$ times its length ; setae *J*4 well removed from the anterior margin of the shield . . . **Macronyssus uncinatus** (Canestrini)

Genus *MACRONYSSUS* Kolenati

Macronyssus Kolenati, 1858, *Wien. ent. Monatschr.* **2** : 5.
Lepronyssus Kolenati, 1858, *Wien. ent. Monatschr.* **2** : 5.
Allonyssus Buitendijk, 1945, *Zool. Med.* **24** : 307 (**syn. nov.**).
Hirstesia Fonseca, 1948, *Proc. zool. Soc. Lond.* **118** : 267.

Type : *Caris longimana* Kolenati, 1857.

Chelicerae chelate, essentially edentate, fixed digit of the female usually produced distally into an acuminate lobe and with up to three retrose denticular processes in its distal half ; movable digit with a strong dorsal hyaline flap usually with denticular processes in its anterior half. Movable digit of male with a grooved spermadactyl, its free portion extending beyond the tip of the digit by about the length of the digit, rarely longer (*M. ellipticus*). Pilus dentilis apparently absent, dorsal seta present, fissures normal. Arthrodial processes absent or in the form of microprocesses. Chaetotaxy of venter of gnathosoma normal, pedipalp with five free segments and a two-tined apotele. Chaetotaxy of pedipalps, trochanter to tibia (2–5–6–14), rarely (2–5–6–13) as in *M. ellipticus*. Palptrochanter with a conspicuous ventral keel. Deutosternum with 8–12 rows of denticles arranged in a single file, or some rows comprising two to five denticles. Corniculi membranous, internal malae simple. Tectum capituli elongate, tapering distally to an obtuse point.

Entire dorsal shield with 21–28 pairs of setae in the female, 21–29 pairs in the male ; paravertical setae (*z*1) absent.

Tritosternum normal, bipartite, lacking denticulate hyaline border. Sternal shield of the female with three pairs of setae and two pairs of pores. " Porose " areas present in the region of the first pair of sternal pores, weakly or strongly defined. Genital shield tapering posteriorly and with genital setae only ; weakly sclerotized area extending from posterior margin of the genital shield with one to several setae in some species. Anal shield pear-shaped, with normal chaetotaxy ; region posterior to postanal seta often markedly elongated. Metapodal shields poorly defined. Opisthogastric cuticle shows hypertrichy. Peritrematal shields fused with the podal shields posterior to coxae IV. Podal shields weakly developed. Male with holoventral shield, with sternito-genital and ventro-anal or with sternito-genital, ventral and ventro-anal shields. Presternal area in both sexes weakly sclerotized.

Chaetotaxy of legs normal except genu IV which has two ventral setae (2—$\frac{2}{1}$, $\frac{3}{1}$—1). Coxa II with prominent anterior spine. Sclerotized ridges of varying degrees of development usually present on ventral surfaces of coxae II–IV. All ambulacra with well-developed claws.

Protonymph with dorsum of idiosoma normally bearing 29 pairs of setae. Podonotal shield with ten pairs of setae, verticals on the integument. Pygidial shield with seven pairs of setae. Normal complement of setae reduced by absence of one or two pairs of setae on the pygidial shield, or increased by hypertrichy of lateral unsclerotized integument. Venter with three pairs of sternal setae, one pair of genital and four pairs of opisthogastric setae. Opisthogaster may show hypertrichy. Anal shield with normal complement of setae. Gnathosoma essentially as in female. Chaetotaxy of legs and pedipalps normal.

Key to Females

1 Opisthonotal region of the dorsal shield with nine pairs of setae (*J* series deficient, Text-fig. 76A) ; majority of deutosternal denticles compound (Text-fig. 76C) . . . 2

– Opisthonotal region of the dorsal shield with 12 pairs of setae ; deutosternal denticles simple, in a single file (Text-fig. 77B) 3

2 Sternal " porose " areas weakly defined, irregular (Text-fig. 76B) ; peritreme reduced, extending to the level of the posterior third of coxa II ; podonotal region with 12 pairs of setae, *j*1 on integument (Text-fig. 76A) . . . **M. ellipticus** (Kolenati) (p. 306)

– Sternal " porose " areas conspicuous, subcircular, bordered by a sclerotized ring (Text-fig. 81B) ; pertreme extending to the level of the middle of coxa I ; podonotal region with 14 pairs of setae, *j*1 on shield (Text-fig. 81A) **M. uncinatus** (Canestrini) (p. 315)

3 Bases of setae *z*6, *Z*1 and *S*1 lying more or less in a straight line (Text-fig. 80A) ; sternal " porose " areas as in Text-fig. 80B ; lateral and opisthogastric cuticle moderately setose. . . . . . **M. kolenatii** (Oudemans) (p. 312)

– Seta *z*6, *Z*1 and *S*1 forming more or less the points of an equilateral triangle (Text-fig. 78A) ; sternal " porose " areas as in Text-fig. 78B ; lateral and opisthogastric cuticle densely setose . . . . . . **M. flavus** (Kolenati) (p. 308)

Key to Males

1 Spermadactyl extremely long, about as long as the second cheliceral segment **M. ellipticus** (Kolenati) (p. 306)

– Spermadactyl obviously shorter in length than the second cheliceral segment . . 2

2 Three pairs of dorsal marginal setae stout, thorn-like ; ventral sclerotization comprising separate sternito-genital, ventral and ventro-anal shields **M. uncinatus** (Canestrini)

– None of the marginal setae conspicuously enlarged ; without separate ventral shield 3

3 Sternito-genital and ventro-anal shield distinctly separated (Text-fig. 78D) ; unsclerotized dorsal integument with numerous short setae (Text-fig. 78C) **M. flavus** (Kolenati) (p. 310)

– With a holoventral shield ; sternito-genital and ventro-anal regions connected at the level of the posterior margin of coxae IV (Text-fig. 80D) ; unsclerotized dorsal integument with about seven pairs of setae **M. kolenatii** (Oudemans) (p. 314)

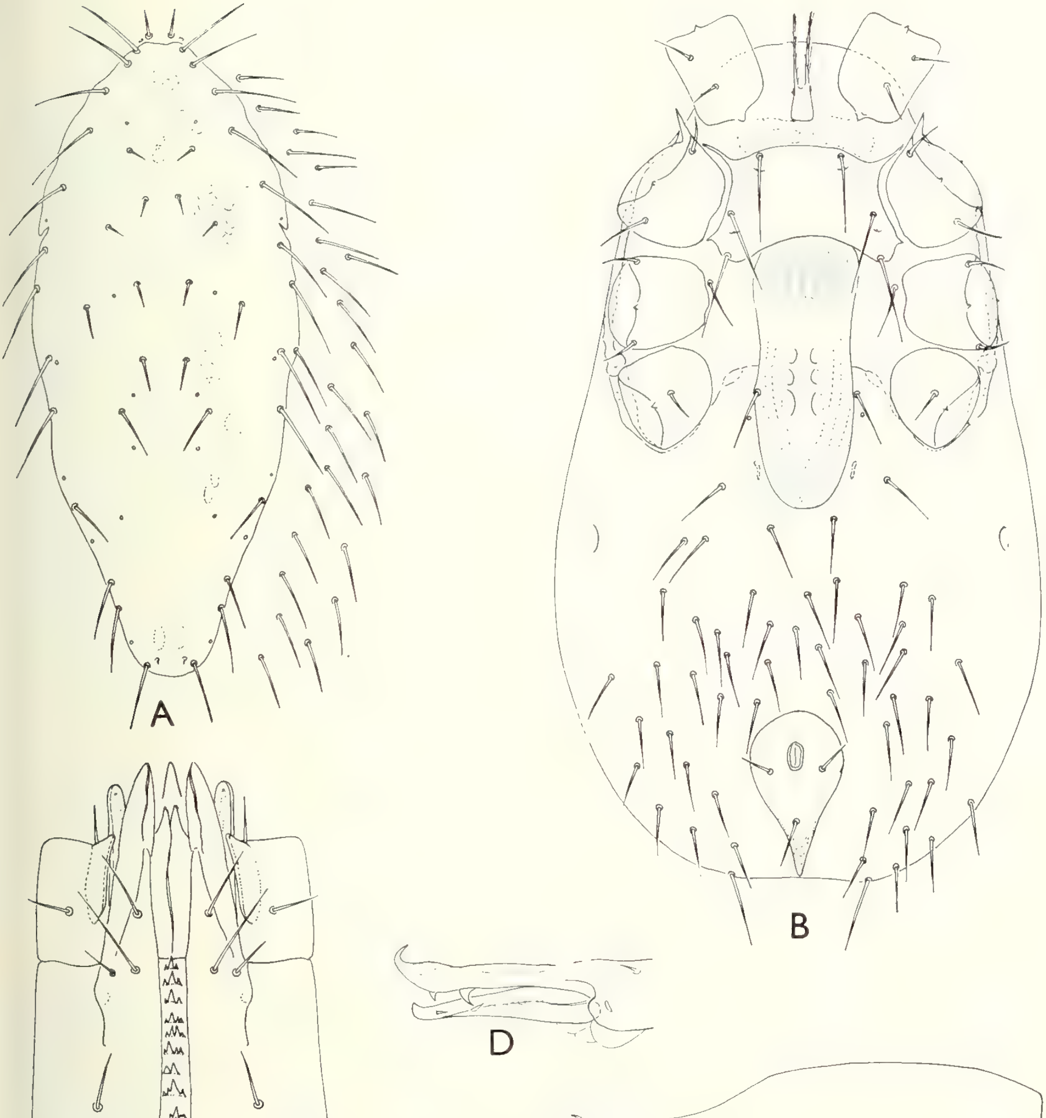

FIG. 76. *Marconyssus ellipticus* (Kolenati), female ; dorsal shield (A) ; venter of idiosoma (B) ; venter of gnathosoma (C) ; chelicera (D–E).

Macronyssus ellipticus (Kolenati)

Caris elliptica Kolenati, 1857, *Parasit. Chiropt.* : 16.
Liponyssus ellipticus: Hirst, 1922, *Proc. zool. Soc. Lond.* (1921) : 795, fig. 36.
Ichoronyssus mohrae Vitzthum, 1932, *Z. Parasitenk.* **4** : 32.

Female : Chelicera with segment I, 45 μ ; II, 170 μ ; movable digit 42 μ long, hooked terminally, dorsal hyaline flap with two denticulate processes. Fixed digit with two denticulate processes and a pointed distal process which appears variously shaped depending on the orientation of the chelicera (Text-figs. 76D and E). Pilus dentilis absent, dorsal seta present. Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 45 μ apart. Deutosternum with 12 transverse rows of denticles (two to five denticles per row). Corniculi membranous, internal malae simple, tectum capituli tapering. Pedipalp (2–5–6–13) with two-tined apotele ; palptrochanter with conspicuous ventral keel (Text-fig. 76C).

Dorsal shield (774 μ × 348 μ) with about 20 pairs of setae distributed as in Text-fig. 76A ; setae *j*1 off the shield. Surface of shield with sculptured areas and a weak reticulate pattern. Unsclerotized integument of dorsum hypertrichous.

Tritosternum with base 36 μ , laciniae 114 μ. Sternal shield (105 μ × 174 μ) with irregular punctate areas in the antero-lateral corners ; with three pairs of setae and two pairs of pores ; metasternal setae free. Between *st*1, 80 μ ; between *st*1 and *st*3, 117 μ. Genital shield (135 μ × 102 μ) with genital setae only. Anal shield (117 μ × 100 μ) pear-shaped with strongly arched anterior margin ; paranal setae about 40 μ long, postanal seta about 54 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 76B. Peritreme extends to posterior third of coxa II ; peritrematal shield free anteriorly ; posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs normal except genu IV which has two ventral setae (2—$\frac{2}{1}$, $\frac{3}{1}$—1). Coxa II with prominent anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	120/60	102/66	84/57	144/60
tibia	114/54	84/60	90/54	132/54
tarsus	192/48	162/54	180/48	240/50

Male : Chelicera with segment I, 30 μ ; II, 123 μ ; movable digit 36 μ long, broad, weakly sclerotized ; spermadactyl greatly enlarged, 87 μ long from base of movable digit, boat-shaped. Fixed digit edentate. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.*2 about 42 μ apart. Other gnathosomal features as in female.

Dorsal shield (648 μ × 288 μ) with 26 pairs of setae. Sternito-genital shield (270 μ × 138 μ) with four pairs of long sternal and a pair of short genital setae. Between *st*1, 63 μ ; between *st*1 and *st*3, 110 μ. Ventro-anal shield with irregular lateral margins ; bearing six asymmetrically arranged setae excluding the anals. Paranal setae 33 μ, postanal seta 42 μ long. Peritreme extends to about middle of coxa II.

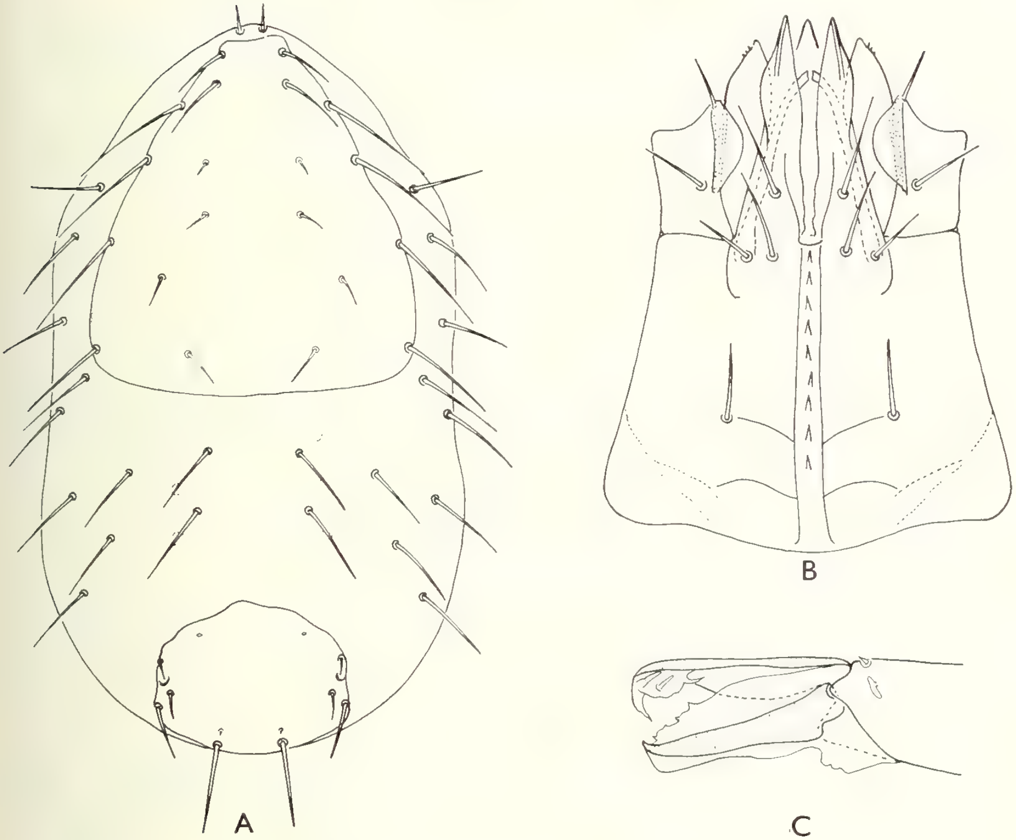

FIG. 77. A. *Macronyssus ellipticus* (Kolenati), protonymph ; dorsum of idiosoma. B–C. *Macronyssus flavus* (Kolenati), female ; venter of gnathosoma (B) ; chelicera (C).

Chaetotaxy of legs as in female. Some relatively long, stout setae on femur I (ad_1 and pd_1) and femur II (ad_1 and pd_{1-2}). Legs bent and not suitable for measurement.

Protonymph : Chelicera with segment I, 30 μ ; II, 114 μ ; movable digit 33 μ. Gnathosoma essentially as in female. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with 12 transverse rows of denticles (one to four denticles per row). Pedipalp (1–4–5–12) with two-tined apotele ; trochanter with conspicuous ventral keel.

Podonotal shield (282 μ × 216 μ) with ten pairs of setae as in Text-fig. 77A ; setae *j*1 situated in front of shield. Pygidial shield (114 μ × 144 μ) with anterior margin convex ; bearing five pairs of setae. Unsclerotized integument of dorsum bears 11 pairs of setae.

Tritosternum with base 30 μ, laciniae 100 μ. Sternal shield (180 μ × 126 μ) with three pairs of setae and two pairs of pores. Between *st*1, 70 μ; between *st*1 and *st*3, 117 μ. Anal shield (66 μ × 66 μ) with paranal setae 36 μ, postanal seta 45 μ long. Peritreme extends to middle of coxa III.

Chaetotaxy of legs normal. Coxa II with conspicuous anterior spine. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	70/52	66/54	54/48	75/48
tibia	66/45	51/48	48/45	68/45
tarsus	120/40	90/40	90/40	135/40

HABITAT: Ectoparasitic on *Myotis myotis* (Borkhausen), *M. daubentonii* (Kuhl) and *M. nattereri* (Kuhl) in Suffolk, England. Recorded from *Myotis* species and also from *Rhinolophus ferrumequinum* (Schreber), *R. hipposideros* (Bechstein) and *Plecotus auritus* (Linn.) in Europe.

Macronyssus flavus (Kolenati)

Dermanissus flavus Kolenati, 1857, *Parasit. Chiropt.* : 19.
Lepronyssus flavus Kolenati, 1859, *S.B. Akad. Wiss. Wien.* **35** : 184.
Liponyssus flavus: Hirst, 1922, *Proc. zool. Soc. Lond.* : 791, figs. 34–35.
Liponyssus lobatus : Oudemans, 1903, *Tijdschr. Ned. dierk. Vereen.* (2) **8** : 18, figs. (non Kolenati, 1857).
Liponyssus britannicus Radford, 1941, *Parasitology* **33** : 311.

Female: Chelicera with segment I, 42 μ; II, 144 μ; movable digit 45 μ long, with a dorsal, hyaline flap which is irregularly denticulate in its anterior half. Fixed digit with an acuminate terminal lobe and three retrose denticular processes in its distal half (Text-fig. 77C). Pilus dentilis absent, dorsal seta minute. Four pairs of gnathosomal setae with *c.s.* 50 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with nine denticles arranged in a single file. Corniculi membranous, internal malae simple. Tectum capituli elongate, pointed distally. Pedipalp (2–5–6–14) with two-tined apotele. Palptrochanter with a conspicuous ventral keel (Text-fig. 77B).

Dorsal shield (624 μ × 288 μ) with 28 pairs of simple setae distributed as in Text-fig. 78A. Surface of shield reticulated. Unsclerotized integument of dorsum shows marked hypertrichy.

Tritosternum with base 33 μ, laciniae 105 μ. Sternal shield (66 μ × 168 μ) with a distinct reticulate pattern in the antero-lateral corners, bearing three pairs of setae and two pairs of pores; metasternal setae free with associated pores. Between *st*1, 54 μ; between *st*1 and *st*3, 96 μ. Genital shield (117 μ × 84 μ) with an overall reticulate pattern, bearing one pair of genital setae. Anal shield (90 μ × 96 μ) with par- and postanal setae about 24 μ long. Sclerotization and chaetotaxy of opistho-

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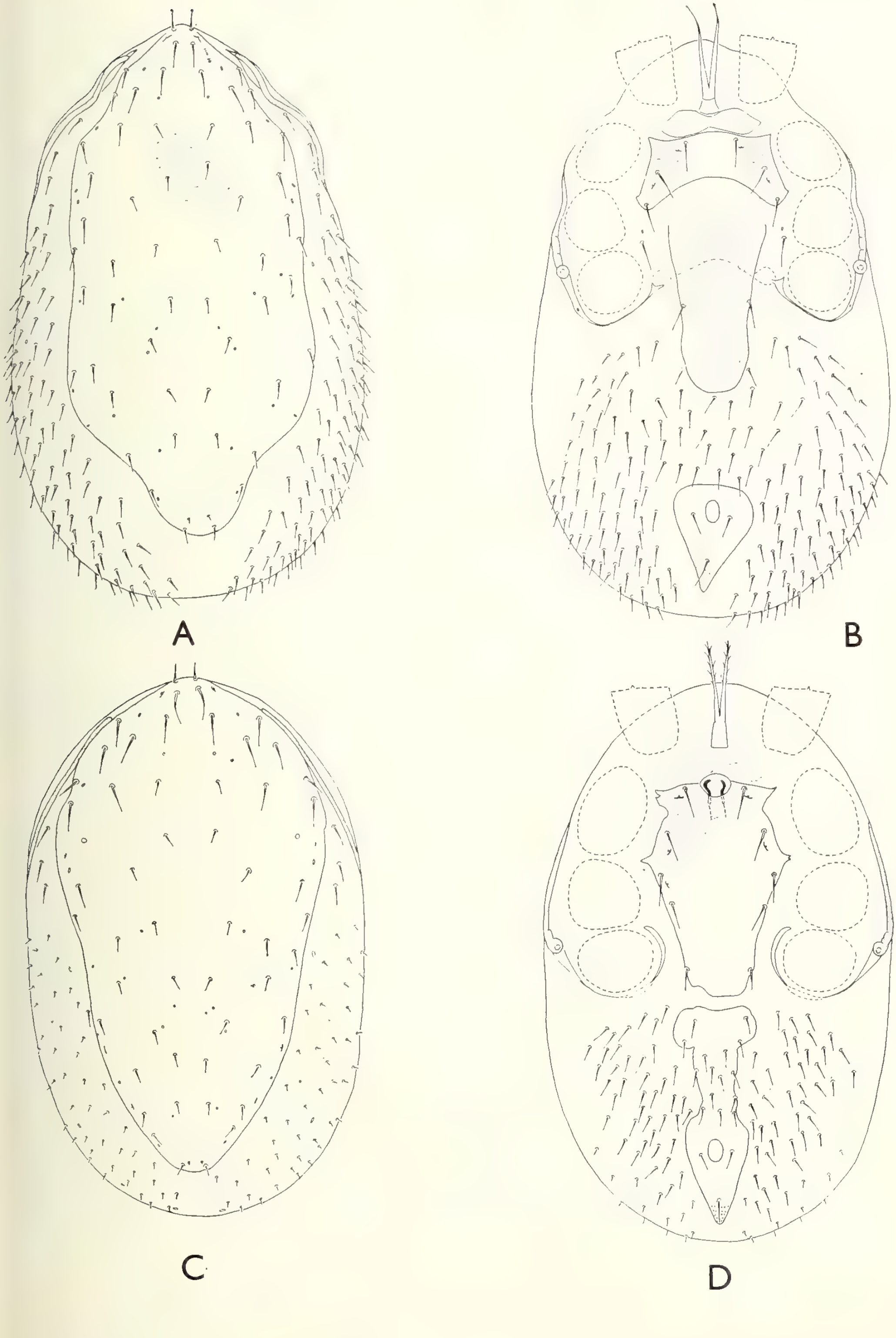
FIG. 78. *Macronyssus flavus* (Kolenati). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. dorsum of idiosoma of male; D. venter of idiosoma of male.


A
B
C
D

gaster as in Text-fig. 78B. Peritreme extends to anterior third of coxa I ; peritrematal shield free anteriorly ; posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs normal except genu IV which has two ventral setae (2—$\frac{2}{1}$, $\frac{3}{1}$—1). Coxae II with large anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	72/50	72/57	48/45	66/45
tibia	72/45	58/54	48/45	60/42
tarsus	105/40	70/48	78/42	126/40

Male : Chelicera with segment I, 24 μ ; II, 81 μ ; movable digit 30 μ long, strongly hooked terminally ; spermadactyl grooved, 45 μ long from base of movable digit. Fixed digit edentate. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp.*2 about 38 μ apart. Other gnathosomal features as in female.

Dorsal shield (540 μ × 252 μ) with 27 or 28 pairs of setae as in Text-fig. 78C. Unsclerotized integument of opisthonotum bears numerous very short, fine setae.

Tritosternum with base 20 μ, laciniae 96 μ. Sternito-genital shield (240 μ × 129 μ) reticulated, with five pairs of setae and three pairs of pores. Between *st*1, 63 μ ; between *st*1 and *st*3, 96 μ. Ventro-anal shield (204 μ × 66 μ) with about fifteen setae excluding the anals ; par- and postanal setae about 20 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 78D. Peritreme extends to middle of coxa I ; peritrematal shield fused anteriorly with dorsal shield ; posterior part fused with podal elements of coxa IV.

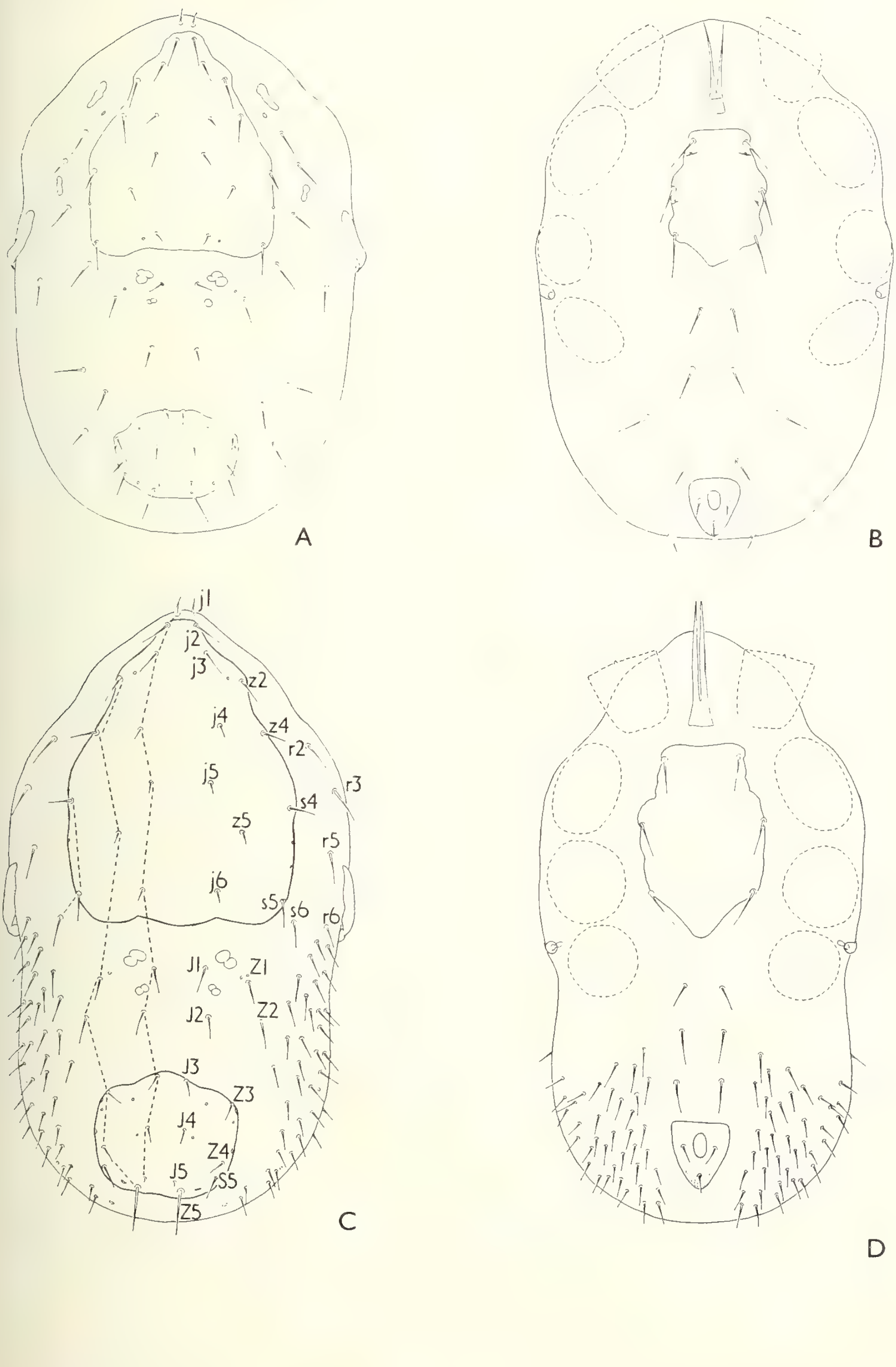
Chaetotaxy of legs as in female. Leg II with some setae situated on small tubercles (anterior seta on coxa ; *av* on femur ; av_1, pv_1 and *mv* on tarsus). Setae *pd* and pv_1 on genu IV and dorsal setae on femur IV stout and spine-like. Coxa II with anterior spine. Length/width (in μ) of leg segments not measurable in the single male we have examined.

Protonymph : Chelicera with segment I, 30 μ ; II, 110 μ ; movable digit 33 μ. Four pairs of gnathosomal setae with *c.s.* about 36 μ apart ; *hyp.*2 about 30 μ apart. Pedipalp (1–4–5–12) with two-tined apotele. Other gnathosomal features as in female.

Podonotal shield (240 μ × 162 μ) with ten pairs of setae (Text-fig. 79C), *j*1 situated on the unsclerotized integument. Pygidial shield slightly wider than long, with seven pairs of setae. Two pairs of mesonotal scutellae present between the anterior and posterior dorsal shields. Unsclerotized integument of opisthonotum markedly hypertrichous.

Tritosternum with base 26 μ, laciniae 84 μ. Sternal shield (150 μ × 100 μ) with three pairs of setae and two pairs of pores. Between *st*1, 54 μ ; between *st*1 and *st*3, 105 μ. Anal shield (42 μ × 48 μ) with par- and postanal setae about 15 μ long.

FIG. 79. A–B. *Macronyssus kolenatii* (Oudemans), protonymph ; dorsum (A) and venter (B) of idiosoma. C–D. *Macronyssus flavus* (Kolenati), protonymph ; dorsum (C) and venter (D) of idiosoma.


A
B
j1
j2
j3
z2
j4
z4
r2
r3
j5
s4
z5
r5
j6
s5
s6
r6
J1
Z1
J2
Z2
J3
Z3
J4
Z4
J5
S5
Z5
C
D

Chaetotaxy of opisthogaster as in Text-fig. 79D. Peritreme extends to about middle of coxa III.

Chaetotaxy of legs normal. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	50/50	45/50	36/45	42/40
tibia	48/45	40/48	36/42	42/40
tarsus	60/40	60/38	54/36	72/36

HABITAT : An ectoparasite of the common Noctule Bat, *Nyctalus noctula* (Schreber), in Britain and Europe.

Macronyssus kolenatii (Oudemans)

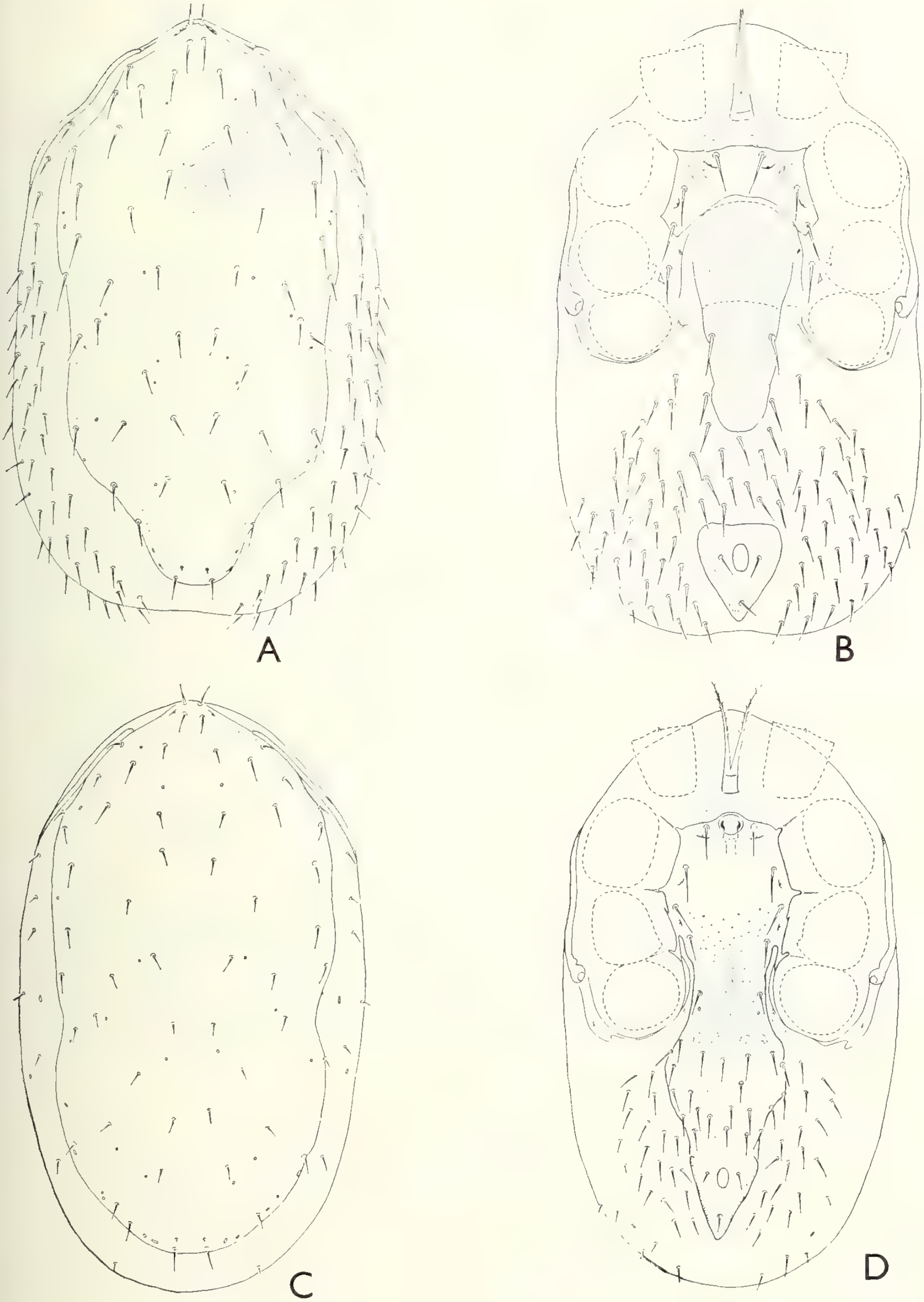
Liponyssus kolenatii Oudemans, 1902, *Ent. Ber. Amst.* **1** (8) : 48 et 1903, *Tijdschr. Ned. dierk. Vereen.* (2) **8** : 25, figs.
Liponyssus pipistrelli Oudemans, 1906, *Ent. Ber. Amst.* **2** (27) : 37 (non Oudemans, 1904).
Liponyssus cyclaspis Oudemans, 1906, *Ent. Ber. Amst.* **2** (28) : 61 (nom. nov. pro *L. pipistrelli* Oudemans, 1906) et 1915, *Arch. Naturgesch.* **81** (A) : 165, figs. 128–134.
Hirstesia britteni Radford, 1953, *Parasitology* **42** : 239.

Female : Chelicera with segment I, 33 μ ; II, 130 μ ; movable digit 42 μ, distal end of dorsal hyaline flap thorn-like and usually bent at right angles to chela ; fixed digit with slender denticular processes. Pilus dentilis absent. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.*2 about 33 μ apart. Deutosternum with eight denticles arranged in a single file. Corniculi membranous, internal malae simple, tectum capituli tapering to an obtuse point. Pedipalp (2–5–6–14) with two-tined apotelele; palptrochanter with a conspicuous ventral keel.

Dorsal shield (540 μ × 252 μ) with 28 pairs of setae distributed as in Text-fig. 80A. Surface of shield reticulated. Unsclerotized integument of dorsum hypertrichous.

Tritosternum with base 21 μ, laciniae 84 μ. Presternal area reticulated. Sternal shield (57 μ × 129 μ) with a pair of elliptical, finely striated areas in the anterolateral corners ; with three pairs of setae and two pairs of pores ; metasternal setae free with associated pores. Between *st*1, 45 μ ; between *st*1 and *st*3, 78 μ. Genital shield (90 μ × 70 μ) reticulated, bearing a pair of genital setae and with an unpaired seta situated on a weakly sclerotized posterior extension of the shield. Anal shield (75 μ × 75 μ) with anterior margin almost straight ; paranal setae 21 μ, postanal seta 24 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 80B. Peritremes extend to middle of coxae I ; peritrematal shields free anteriorly, fused posteriorly with podal elements of coxae IV.

FIG. 80. *Macronyssus kolenatii* (Oudemans). A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. dorsum of idiosoma of male ; D. venter of idiosoma of male.


A
B
C
D

Chaetotaxy of legs normal except genu IV which has two ventral setae (2—$\frac{2}{1}$, $\frac{3}{1}$—1). Femur I with setae ad_1 and pd_1 long and stout. Coxa II with large, pointed anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	63/48	60/54	38/45	54/45
tibia	54/45	45/50	36/42	50/42
tarsus	72/40	78/40	60/40	80/38

Male : Chelicera with segment I, 36 μ ; II, 87 μ ; movable digit 30 μ long, edentate ; spermadactyl grooved, about 45 μ long from base of movable digit. Fixed digit edentate. Four pairs of gnathosomal setae with *c.s.* about 40 μ apart, *hyp.2* about 33 μ apart. Deutosternum with 10 denticles arranged in a single file ; corniculi about 36 μ long, membranous. Other gnathosomal features as in female.

Dorsal shield (504 μ × 270 μ) with 28 or 29 pairs of setae distributed as in Text-fig. 80C. Unsclerotized integument of dorsum with seven pairs of setae.

Tritosternum with base 27 μ, laciniae 90 μ. Holoventral shield (380 μ × 105 μ) with five pairs of setae in the sternito-genital region and about 20 setae in the ventral region. Between *st1*, 45 μ ; between *st1* and *st3*, 81 μ. Paranal and postanal setae about 18 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 80D. Peritremes extend to middle of coxae I ; peritrematal shields fused anteriorly with dorsal shield, posteriorly with podal elements of coxae IV.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	66/45	60/50	40/40	54/40
tibia	54/40	45/45	36/36	48/38
tarsus	69/33	50/36	54/33	75/34

Protonymph : Chelicera with segment I, 15 μ ; II, 72 μ ; movable digit 27 μ. Gnathosomal features essentially as in female. Capitular setae about 30 μ apart, *hyp.2* about 27 μ apart. Pedipalp (1–4–5–12) with two-tined apotele.

Podonotal shield (180 μ × 147 μ) with 10 pairs of setae as in Text-fig. 79A ; setae *j1* in front of shield. Pygidial shield (72 μ × 99 μ) with seven pairs of setae. Two pairs of mesonotal scutellae present. Unsclerotized integument of dorsum with eleven pairs of setae (excluding *j1*).

Tritosternum with base 21 μ, laciniae 54 μ. Sternal shield (110 μ × 75 μ) with three pairs of setae and two pairs of pores. Between *st1*, 42 μ ; between *st1* and *st3*, 75 μ. Anal shield (36 μ × 39 μ) with par- and postanal setae about 15 μ long. Opisthogaster with five pairs of setae (Text-fig. 79B). Peritremes extend to middle of coxae III.

Chaetotaxy of legs normal. Femur I with setae ad_1 and pd_1 long and thick. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	36/42	36/45	24/34	30/34
tibia	36/36	30/39	21/34	30/34
tarsus	45/30	42/30	39/27	51/27

HABITAT: An ectoparasite on bats of the genus *Pipistrellus*. Recorded from *P. pipistrellus* (Schreber) in Britain and Europe and from *P. kuhli* (Kuhl) in Egypt.

Macronyssus uncinatus (Canestrini)

Leiognathus uncinatus Canestrini, 1885, *Acarofauna ital.* **1**: 122; Berlese, 1889, *Acar. Myr. Scorp. Ital.* fasc. 53, no. 7.
Liponyssus rhinolophi Oudemans, 1902, *Tijdschr. Ned. dierk. Vereen.* (2) **7**: 65.
Liponyssus sternalis Hirst, 1922, *Proc. zool. Soc. Lond.* (1921): 781, figs. 25–26.

Female: Chelicera with segment I, 54 μ; II, 150 μ; movable digit 40 μ long, truncate tip with acute dorsal angle. Fixed digit with two slender, subequal, denticular processes. Pilus dentilis absent. Four pairs of gnathosomal setae with *c.s.* about 63 μ apart; *hyp.*2 about 45 μ apart. Deutosternum with 10–12 rows of denticles (1–4, usually one or two denticles per row). Corniculi membranous, internal malae simple. Pedipalp (2–5–6–14) with two-tined apotele; palptrochanter with conspicuous ventral keel.

Dorsal shield (798 μ × 372 μ) with 25 pairs of setae distributed as in Text-fig. 81A. Marginal setae of podonotal region of shield conspicuously longer than setae *j4–j6* and *z5–z6*. Surface of shield granular and weakly reticulated; unsclerotized integument of opisthonotum hypertrichous.

Tritosternum with base 54 μ, laciniae 132 μ. Sternal shield (84 μ × 180 μ) with a pair of rounded porose areas each surrounded by a heavily sclerotized margin. The shield bears three pairs of setae and two pairs of pores; metasternals free with associated pores. Between *st*1, 72 μ; between *st*1 and *st*3, 105 μ. Genital shield (150 μ × 90 μ) with a weakly sclerotized extension of its tip bearing from one to a maximum of five opisthogastric setae. Anal shield (130 μ × 96 μ) with paranal setae about 45 μ long, postanal seta 60 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 81B. Peritreme extends to middle of coxa I; peritrematal shield free anteriorly, posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs normal except genu IV which has two ventral setae (2—$\frac{2}{1}$, $\frac{3}{1}$—1). Coxa II with pronounced anterior spine. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	114/78	120/78	102/72	150/72
tibia	114/70	96/72	90/72	144/66
tarsus	210/60	174/60	198/63	288/60

Male and protonymph: Described by Dusbabek (1964).

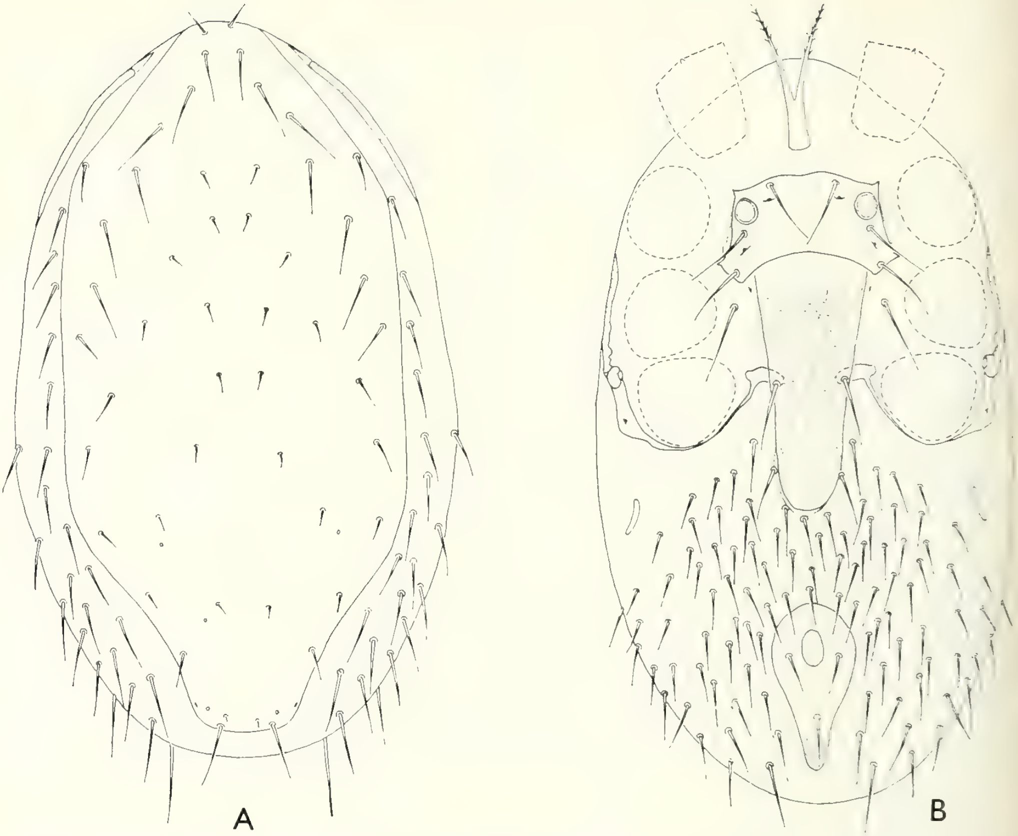


FIG. 81. *Macronyssus uncinatus* (Canestrini), female; dorsum (A) and venter (B) of idiosoma.

HABITAT: An ectoparasite of bats. Reported from *Rhinolophus hipposideros* (Bechstein) in Britain and from *R. ferrumequinum* (Schreber), *R. euryale* Blasius, *Pipistrellus pipistrellus* (Schreber), *Myotis emarginatus* (Geoffroy) and *Miniopterus schreibersi* (Natterer) in Europe.

Genus ***ORNITHONYSSUS*** Sambon

Leiognathus Canestrini, 1884, *Atti ist. Veneto* (6) **2**: 1573 (nom. preocc.).
Ornithonyssus Sambon, 1928, *Ann. trop. Med. Parasit.* **22**: 105.
Bdellonyssus Fonseca, 1941, *Cienca* **2**: 262.
Fonsecaonyssus Radford, 1950, *Parasitology* **40**: 373.

Type: *Dermanyssus sylviarum* Canestrini and Fanzago, 1877.

Chelicerae chelate, edentate, without denticular processes; fixed digit in the female terminating in a hyaline boss. Spermadactyl grooved, free distally, relatively short. Pilus dentilis absent, dorsal seta minute, fissures present. Arthrodial processes absent. Chaetotaxy of venter of gnathosoma normal, pedipalps with five free segments and a two-tined apotele. Chaetotaxy of palptrochanter to tibia (2–5–6–13), rarely (2–5–6–12). Seta *pl* on palpfemur of male usually situated on a tubercle. Palptrochanter usually with an antero-ventral keel in the females, rarely in the males. Deutosternum with 9–11 denticles arranged in a single file. Corniculi membranous, internal malae simple, free or fused. Tectum elongate, tapering to an obtuse or acute point, lateral margins smooth or weakly denticulate.

Dorsal idiosomal sclerotization reduced in the female and normally comprising an entire dorsal shield strongly tapering behind the level of *j*6 and *z*6, rarely with podonotal shield bearing ten pairs of podonotal setae and one pair of opisthonotal setae (*J*1), and a separate pygidial shield with two pairs of setae (*O. aridus*). Podonotal region with 10–12 pairs of setae, *j*3 present or absent. Opisthonotal region with 6–11 pairs of setae, *J*5 present or absent. Lateral cuticle hypertrichous. Dorsal idiosomal sclerotization in the male more extensive, podonotal region with 10–14 pairs of setae, opisthonotal region with 7–11 pairs. Lateral cuticle less setose than in the female. Dorsal setae smooth or sparsely barbed.

Tritosternum bipartite with hyaline denticulate border. Sternal shield normally with three pairs of setae and two pairs of pores, rarely with two pairs of setae and two pairs of pores (*O. sylviarum*). Genital shield strongly tapering posteriorly with genital setae only. Anal shield normal. Metapodals poorly developed. Opisthogastric cuticle shows hypertrichy. Peritrematal shield fused with podals of coxae IV, free anteriorly. Podal shields weakly developed. Males with slender holoventral shield. Peritrematal shield free or fused anteriorly with the dorsal shield.

Chaetotaxy of legs normal except genu III (2—$\frac{2}{1}$, $\frac{2}{1}$—2), tibia III (2—$\frac{1}{1}$, $\frac{2}{1}$—2) and genu IV (2—$\frac{2}{1}$, $\frac{3}{1}$—1). Rarely genu and tibia I with two ventrals only and genua II and III with one ventral in some populations of *O. sylviarum*. Coxa II with anterior spine sometimes minute. Coxa III with retrograde spur only in *O. pereira;* no sclerotized ridges.

Protonymph with dorsum of idiosoma provided with a podonotal shield bearing 10 (*j*3 lacking) or 11 pairs of setae, two or more pairs of mesonotal scutellae, and a pygidial shield bearing from three to six pairs of setae. The unsclerotized integument of the dorsum usually bears 15 or 16 pairs of setae. Venter with three pairs of sternal setae, one pair of genital and four to five pairs of opisthogastric setae. Anal shield with normal chaetotaxy. Gnathosoma essentially as in female. Chaetotaxy of legs and pedipalps normal. Palptrochanter with or without ventral keel.

The above concept of *Ornithonyssus* is considerably wider than that of Furman & Radovsky (1963). These authors restrict this genus to New World forms, except for four species, *O. bacoti*, *ondatrae*, *sylviarum* and *bursa*, " which have been widely dispersed by human activity ". They correctly point out that the species included in their concept of *Ornithonyssus* differ from Old World forms in both sexes having certain idiosomal setae, particularly the caudal and marginal setae, barbed and seta *pl* on the palpfemur of the male situated on a tubercle. It is possible that the New and Old World species of *Ornithonyssus* s. lat. are not congeneric but their status must await a comprehensive revision of the complex.

KEY TO FEMALES

1 Dorsal shield with setae *j*3 present ; opisthonotal region of shield with eight pairs of setae. Dorsal setae smooth. Peritremes extend to middle of coxae II. First pair of sternal setae about half as long as the second. On bats (*Eptesicus* and *Plecotus*) . . . . **O. pipistrelli** (Oudemans) (p. 326)

– Dorsal shield with setae *j*3 absent ; opisthonotal region of shield with not more than seven pairs of setae. Some dorsal setae barbed. Peritremes extend to posterior margin of coxae I. Sternal setae subequal 2

2 Dorsum with setae *s*4 and *S*5 situated on the shield ; setae of *J* series relatively long, *J*1 reaching base of *J*2 (Text-fig. 83A). Sternal shield with three pairs of setae. Opisthogastric cuticle relatively densely setose (Text-fig. 83D). Palptibia with 13 setae. On small mammals . . . . . . **O. bacoti** (Hirst) (p. 321)

– Dorsum with setae *s*4 and *S*5 not on the shield ; setae of *J* series relatively short, *J*1 extending less than half way to base of *J*2 (Text-fig. 82A). Sternal shield with two pairs of setae. Opisthogastric cuticle relatively sparsely setose (Text-fig. 82B). Palptibia with 12 setae. On birds **O. sylviarum** (Canestrini & Fanzago) (p. 318)

KEY TO MALES

1 Dorsal shield with 14 pairs of setae in the podonotal region. Coxae II and III with anterior setae stout and spine-like. Palpfemur with seta *pl* normal, not situated on a tubercle. On bats (*Eptesicus* and *Plecotus*) **O. pipistrelli** (Oudemans) (p. 326)

– Dorsal shield with 10 or 11 pairs of setae in podonotal region. Coxae II and III with anterior setae normal. Palpfemur with seta *pl* situated on a tubercle . . 2

2 Dorsum with seta *S*5 on shield. Setae of *j* series relatively long, seta *j*4 reaching base of *j*5. Holoventral shield with eight pairs of setae, excluding anals. Palptibia with 13 setae. On small mammals . . . . . . **O. bacoti** (Hirst) (p. 323)

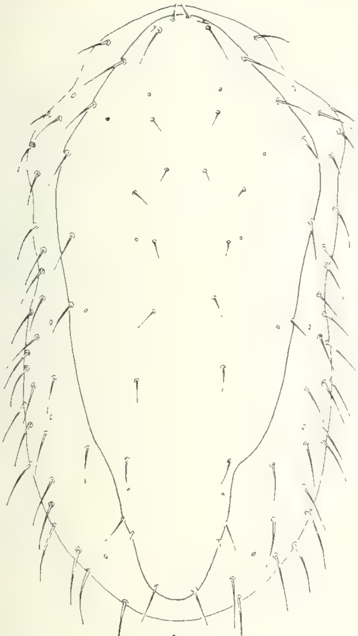
– Dorsum with seta *S*5 not on the shield. Setae of the *j* series relatively short, seta *j*4 reaching half-way to base of *j*5. Holoventral shield with six pairs of setae, excluding anals. Palptibia with 12 setae. On birds **O. sylviarum** (Canestrini & Fanzago) (p. 320)

Ornithonyssus sylviarum (Canestrini & Fanzago)

Dermanyssus sylviarum Canestrini & Fanzago, 1877, *Atti Ist. Veneto* **5** : 124.
Liponyssus americanus Banks, 1906, *Proc. ent. Soc. Wash.* **8** : 136.
Liponyssus canadensis Banks, 1909, *Proc. ent. Soc. Wash.* **11** : 134.
Liponyssus pacificus Ewing, 1923, *Proc. U.S. nat. Mus.* **62** (art. 13) : 19.

Female : Chelicera with segment I, 20 μ ; II, 150 μ ; movable digit 36 μ long, with a dorsal " trough " ; both digits edentate ; pilus dentilis and arthrodial processes absent. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.2* about 36 μ apart. Deutosternum with about 10 denticles arranged in a single file. Corniculi membranous ; internal malae with inner processes fused, outer leaf-like. Tectum capituli tapers to a sharp point, margin weakly denticulate. Pedipalp (2–5–6–12) with two-tined apotele ; palptrochanter with small ventral keel.

FIG. 82. *Ornithonyssus sylviarum* (Canestrini and Fanzago). A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. venter of idiosoma of male ; D. dorsum of idiosoma of protonymph.



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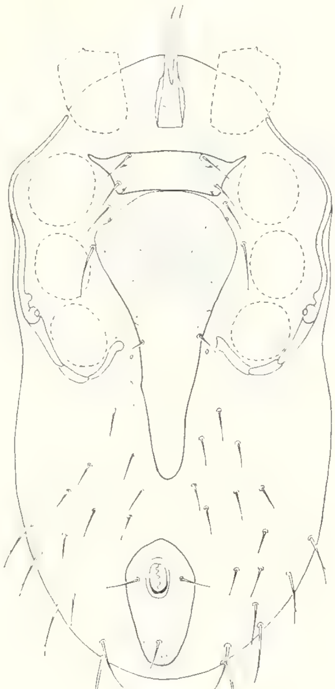

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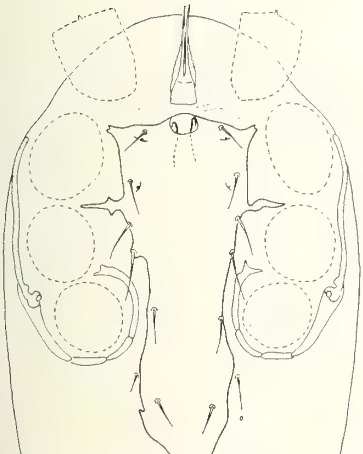

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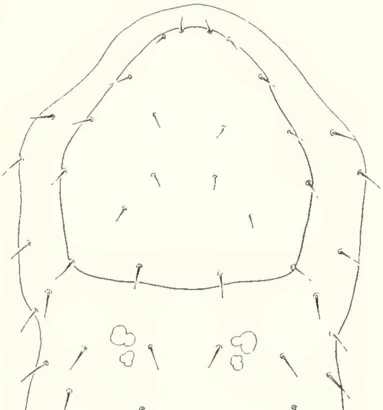

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Dorsal shield (534 μ × 228 μ) usually with 17 pairs of setae distributed as in Text-fig. 82A; one or more of the setae in the opisthonotal region may be absent. Unsclerotized integument of dorsum hypertrichous.

Tritosternum with hyaline denticulate membrane, base 42 μ, laciniae 75 μ. Sternal shield (36 μ × 100 μ) reticulated and bearing two pairs of setae and two pairs of pores; *st*3 and *st*4 on unsclerotized cuticle. Between *st*1, 66 μ; between *st*1 and *st*3, 52 μ. Genital shield (132 μ × 60 μ) tapering, with genital setae only. Anal shield (96 μ × 66 μ) with par- and postanal setae subequal, about 30 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 82B. Peritremes extend to posterior margin of coxae I; peritrematal shields free anteriorly, fused posteriorly with podal elements of coxae IV.

Chaetotaxy of legs generally normal except genu III ($2—\frac{2}{1}, \frac{2}{0/1}—2$), tibia III ($2—\frac{1}{1}, \frac{2}{1}—2$) and genu IV ($2—\frac{2}{1}, \frac{3}{1}—1$). In addition, one of the ventral setae may be lacking on genu I ($2—\frac{3}{1/2}, \frac{3}{1}—2$), tibia I ($2—\frac{3}{1/2}, \frac{3}{1}—2$) and genu II ($2—\frac{3}{1}, \frac{2}{0/1}—2$) in some specimens. Coxa II without anterior spine. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	60/38	54/45	48/36	60/33
tibia	60/34	50/38	48/33	63/33
tarsus	110/34	90/36	96/30	130/30

Male: Chelicera with segment I, 20 μ; II, 90 μ; movable digit 27 μ long; both digits edentate; spermadactyl 36 μ long from base of movable digit. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.*2 about 36 μ apart. Deutosternum with ten denticles arranged in a single file. Corniculi membranous; internal malae blade-like. Palptrochanter without a ventral keel. Other gnathosomal features as in female.

Dorsal shield (444 μ × 210 μ) with chaetotaxy as in female, except that it may incorporate one or more marginal setae in the opisthonotal region. The short postero-lateral seta (*x*) varies in position; it may be posterior to seta *Z*4 as in the female, level with it or anterior to it. Unsclerotized integument of dorsum hypertrichous.

Tritosternum with base 24 μ, laciniae 57 μ. Holoventral shield (360 μ × 93μ) narrow, with six pairs of setae excluding the anals. Between *st*1, 54 μ; between *st*1 and *st*3, 70 μ. Par- and postanal setae subequal, about 24 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 82C. Peritreme extends to middle of coxa II; peritrematal shields free anteriorly, fused posteriorly with podal shields of coxae IV.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	46/32	45/38	40/33	54/30
tibia	48/30	42/33	38/27	52/28
tarsus	87/27	75/30	75/27	102/27

Protonymph: Chelicera with segment I, 15 μ; II, 105 μ; movable digit 27 μ. Gnathosomal featues generally as in female. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp.*2 about 30 μ apart. Deutosternum with 8 denticles arranged in a single file. Pedipalp (1–4–5–12) with two-tined apotele.

Podonotal shield (162–174 μ × 144–156 μ) with ten pairs of setae distributed as in Text-fig. 82D. Pygidial shield (50 μ × 100 μ) with three pairs of setae, the terminal pair (*Z*5) being at least four times as long as the other setae on the shield. Unsclerotized integument of dorsum with 16 pairs of setae.

Tritosternum with base 24 μ, laciniae 60 μ. Sternal shield (120 μ × 96 μ) with three pairs of setae and two pairs of pores. Between *st*1, 63 μ; between *st*1 and *st*3, 75 μ. Genital setae very short, about half as long as the sternal and the four pairs of opisthogastric setae. Anal shield (42–45 μ × 50–54 μ) with paranal setae about 24 μ, postanal seta about 18 μ long. Peritreme extends to posterior third of coxa III.

Chaetotaxy of legs normal. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	40/36	36/36	32/32	40/30
tibia	42/33	33/33	30/30	42/30
tarsus	78/30	57/27	63/27	84/26

HABITAT: A common parasite of poultry and wild birds in Britain, Europe, U.S.S.R. and North America. It has also been recorded from a number of wild birds in South Africa (Zumpt & Till, 1961).

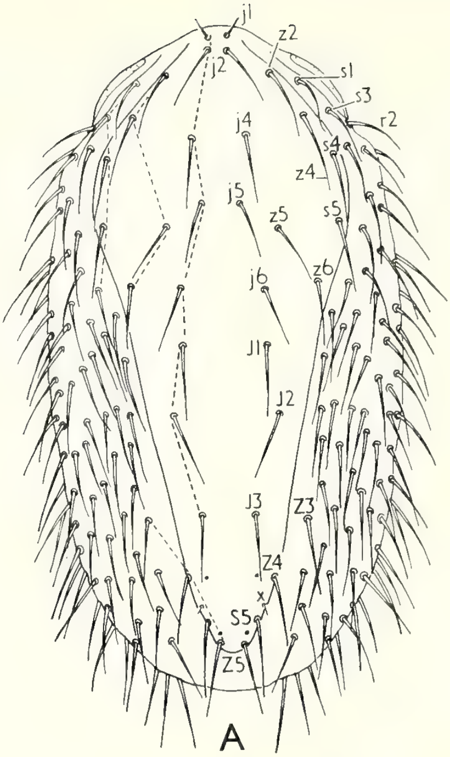
Ornithonyssus bacoti (Hirst)

Leiognathus bacoti Hirst, 1913, *Bull. ent. Res.* **4**: 122 et 1914, *Bull. ent. Res.* **5**: 225, figs. 12–14.
Haemogamasus sanguineus Ewing & Stover, 1915, *Ent. News* **26**: 109.
Liponyssus tenuiscutatus Ewing, 1923, *Proc. U.S. nat. Mus.* **62** (art. 13): 22.
Liponyssus nagayoi Yamada, 1930, *Proc. eighth Congr. Far East Ass. trop. Med.* **2**: 258.

Female: Chelicera with segment I, 33 μ; II, 228 μ; movable digit 50 μ long, with an elliptical " trough " in its dorsal surface. Fixed digit slender, terminating in a hyaline boss. Pilus dentilis and arthrodial processes absent (Text-fig. 83E). Four pairs of gnathosomal setae with *c.s.* about 57 μ apart, *hyp.*2 about 42 μ apart. Deutosternum with about ten denticles arranged in a single file. Corniculi membranous; internal malae fused. Tectum capituli tapering to a point. Pedipalp (2–5–6–13) with two-tined apotele; palptrochanter with an antero-ventral keel.

Dorsal shield (660 μ × 198 μ) with 18 pairs of setae distributed as in Text-fig. 83A. Unslcerotized integument of dorsum hypertrichous.

Tritosternum with hyaline denticulate membrane; base 66 μ, laciniae 108 μ. Sternal shield (50 μ × 120 μ) reticulated, with three pairs of setae and two pairs of pores; metasternals free. Between *st*1, 70 μ; between *st*1 and *st*3, 66 μ. Genital shield (174–180 μ × 70–75 μ) tapering, with genital setae only. Anal shield (123–135 μ × 78–87 μ) with paranal setae 42 μ, postanal seta 45 μ long. Chaetotaxy and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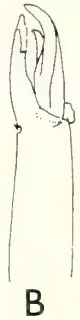
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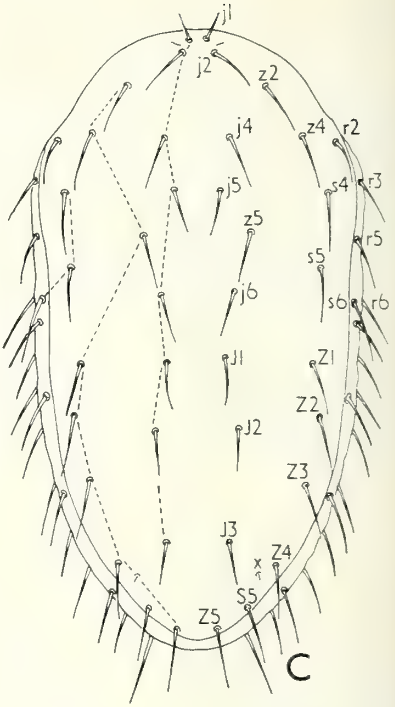
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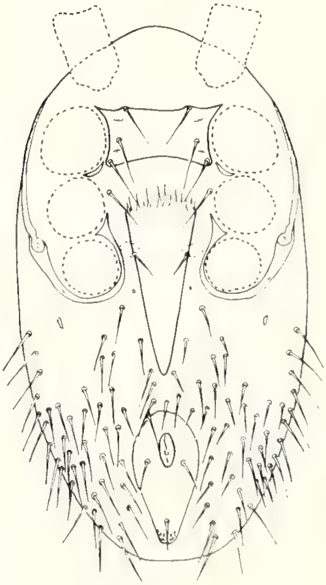
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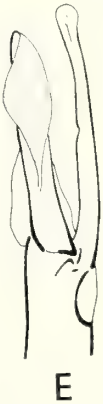
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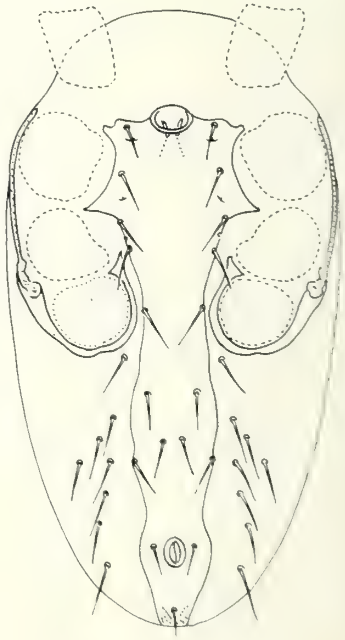
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sclerotization of opisthogaster as in Text-fig. 83D. Peritreme extends to posterior margin of coxa I; peritrematal shield free anteriorly, posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs normal except genu III ($2—\frac{2}{1}, \frac{2}{1}—2$), tibia III ($2—\frac{1}{1}, \frac{2}{1}—2$) and genu IV ($2—\frac{2}{1}, \frac{3}{1}—1$). Coxa II with small anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	96/40	66/45	60/42	84/38
tibia	96/33	66/42	60/40	84/33
tarsus	162/33	120/36	126/34	168/33

Male : Chelicera with segment I, 27 μ; II, 120 μ; movable digit 36 μ; both digits edentate. Spermadactyl relatively short, 45 μ from base of movable digit (Text-fig. 83B). Dorsal seta minute, pilus dentilis and arthrodial processes absent. Four pairs of gnathosomal setae with *c.s.* about 54 μ apart, *hyp.*2 about 38 μ apart. Corniculi membranous; internal malae blade-like, free. Pedipalp as in female, but palptrochanter without ventral keel; seta *pl* on palpfemur situated on a small tubercle.

Dorsal shield (528 μ × 270 μ) with 21 pairs of setae distributed as in Text-fig. 83C. Unsclerotized integument of dorsum much less densely setose than in the female.

Tritosternum with base 36 μ, laciniae 75 μ. Holoventral shield (444 μ × 100 μ) narrow, with eight pairs of setae excluding the anals. Paranal setae 30 μ, postanal seta 33 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 83F. Peritremes extend to posterior margin of coxae I; peritrematal shields fused anteriorly with dorsal shield and posteriorly with podal elements of coxae IV.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	75/40	60/48	60/45	72/36
tibia	78/33	54/48	54/42	75/36
tarsus	130/30	80/40	87/34	120/30

Larva : Chelicera with segment I, 10 μ; II, 63 μ; movable digit 8 μ; both digits simple and edentate. Two pairs of gnathosomal setae (*hyp.*1 and 2) with *hyp.*2 about 24 μ apart. Deutosternal teeth not visible. Corniculi degenerate. Pedipalp (0–3/4–5–10) with two-tined apotele; palptrochanter without keel.

Dorsum with no visible sclerotization; with eight pairs of setae in the podonotal region and three pairs in the opisthonotal region.

Tritosternum bipartite, laciniae strongly reduced, without visible denticulate membrane; base 36 μ, laciniae 24 μ. Sternal region with three pairs of setae, but

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FIG. 83. *Ornithonyssus bacoti* (Hirst). A. Dorsum of idiosoma of female; B. chelicera of male; C. dorsum of idiosoma of male; D. venter of idiosoma of female; E. chelicera of female; F. venter of idiosoma of male.

no visible sclerotization. Opisthogaster with two pairs of setae (*Jv*1 and *Jv*2); three anal setae present, but no definite shield. Stigma and peritreme absent. Chaetotaxy of legs as in free-living Dermanyssidae.

Protonymph: Chelicera with segment I, 24 μ; II, 135 μ; movable digit 33 μ. Gnathosomal features generally as in female. Four pairs of gnathosomal setae with *c.s.* about 36 μ apart, *hyp.*2 about 27 μ apart. Deutosternum with nine denticles arranged in a single file. Pedipalp (1–4–5–12) with two-tined apotele, no keel on palptrochanter.

Podonotal shield (228 μ × 174 μ) with ten pairs of setae as in Text-fig. 84A; pygidial shield (75 μ × 123 μ) with four pairs of setae. Unsclerotized integument of dorsum with 16 pairs of setae.

Tritosternum bipartite, with hyaline denticulate membrane; base 27 μ, laciniae 75 μ. Sternal shield (123 μ × 90 μ) with three pairs of setae and two pairs of pores. Between *st*1, 50 μ; between *st*1 and *st*3, 90 μ. A pair of short genital setae is situated posterior to the sternal shield. Anal shield (60 μ × 42 μ) with paranal setae 30 μ; postanal seta 36 μ long. Opisthogastric cuticle with four pairs of setae, *Jv*1–2, *Jv*5 and *Zv*2 (Text-fig. 84B). Peritreme extends to anterior margin of coxa III.

Chaetotaxy of legs normal. Length/width (in μ) of leg segments:

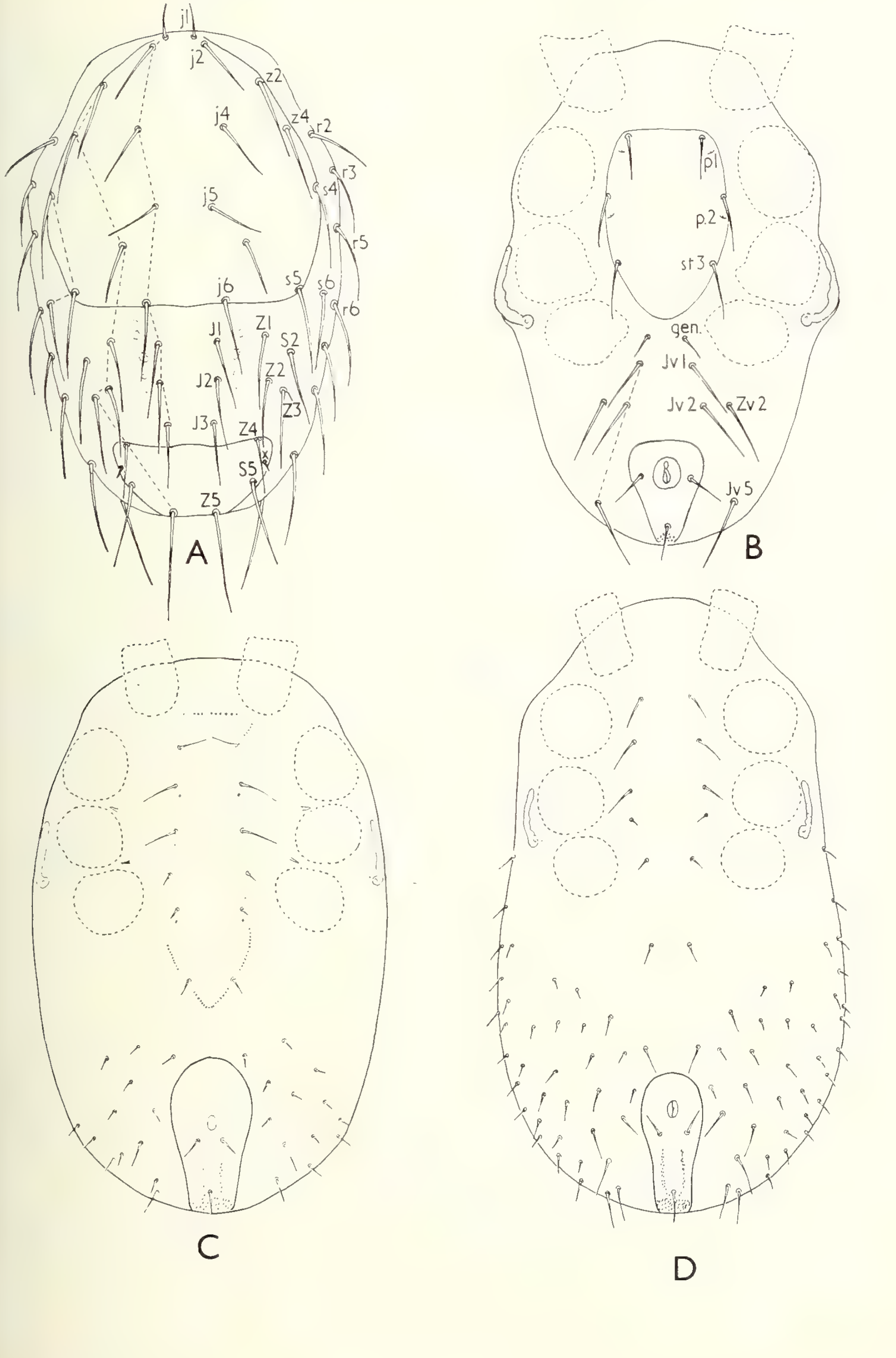
	I	II	III	IV
genu	48/33	42/39	33/33	45/33
tibia	54/30	40/36	33/33	48/30
tarsus	93/27	60/30	60/27	84/27

Deutonymph: Male and female deutonymphs have been distinguished which differ chiefly in their setation, the female being more densely hypertrichous than the male. In both forms the chelicerae have simple edentate digits as in the larva. Deutosternum with ten transverse rows of denticles (one to three denticles per row); internal malae not fused; pedipalp (2–5–6–13) with two-tined apotele.

Dorsum very weakly sclerotized, so that distinct shields are not recognizable. Male with 15 pairs of setae in the podonotal and 22 pairs in the opisthonotal region; female with 23 pairs of setae in the podonotal region, opisthonotal region markedly hypertrichous.

Tritosternum simple, bipartite only at its tip. Area between the coxae with three pairs of relatively long sternal setae, a pair of short metasternal and a pair of short genital setae. The margins of a shield are weakly defined in the male (Text-fig. 84C), but not visible in the female (Text-fig. 84D). Opisthogastric cuticle with 13 pairs of setae in the male, markedly hypertrichous in the female. Par- and postanal setae subequal in length. Peritremes extend to anterior margin of coxae III.

FIG. 84. *Ornithonyssus bacoti* (Hirst). A. Dorsum of idiosoma of protonymph; B. venter of idiosoma of protonymph; C. venter of idiosoma of deutonymph (male); D. venter of idiosoma of deutonymph (female).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x
S5
Z5
A
p1
p.2
st 3
gen.
Jv1
Jv 2
Zv 2
Jv 5
B
C
D

Chaetotaxy of legs as in female.

HABITAT : *O. bacoti*, the tropical rat mite, is apparently of recent introduction to Britain where its distribution is centred mainly around ports. It is essentially a parasite of rodents, especially *Rattus rattus* (Linn.), but is also known to bite man (Evans *et al.*, 1961).

Ornithonyssus pipistrelli (Oudemans)

Liponyssus musculi (Koch) Oudemans, 1902, *Tijdschr. Ned. dierk Vereen.* (2) **8** : 17, pl. 1, figs. 1–2.

Liponyssus pipistrelli Oudemans, 1903, *Tijdschr. Ent.* **46** : 111 [nom. nov. pro *Liponyssus musculi* (Koch) Oudemans, 1902].

Female : Chelicera with segment I, 54 μ ; II, 174 μ ; movable digit 50 μ, edentate with dorsal " trough " ; fixed digit with terminal hyaline boss. Four pairs of gnathosomal setae with *c.s.* about 66 μ apart, *hyp.*2 about 42 μ apart. Deutosternum with nine denticles arranged in a single file. Corniculi membranous ; internal malae with inner processes fused, outer large and leaf-like. Tectum capituli tapering, with serrated margin. Pedipalp (2–5–6–13) with two-tined apotele ; palptrochanter with ventral keel.

Dorsal shield (912 μ × 294 μ) narrow, reticulated, with 20 pairs of setae distributed as in Text-fig. 85A. Unsclerotized integument of dorsum hypertrichous.

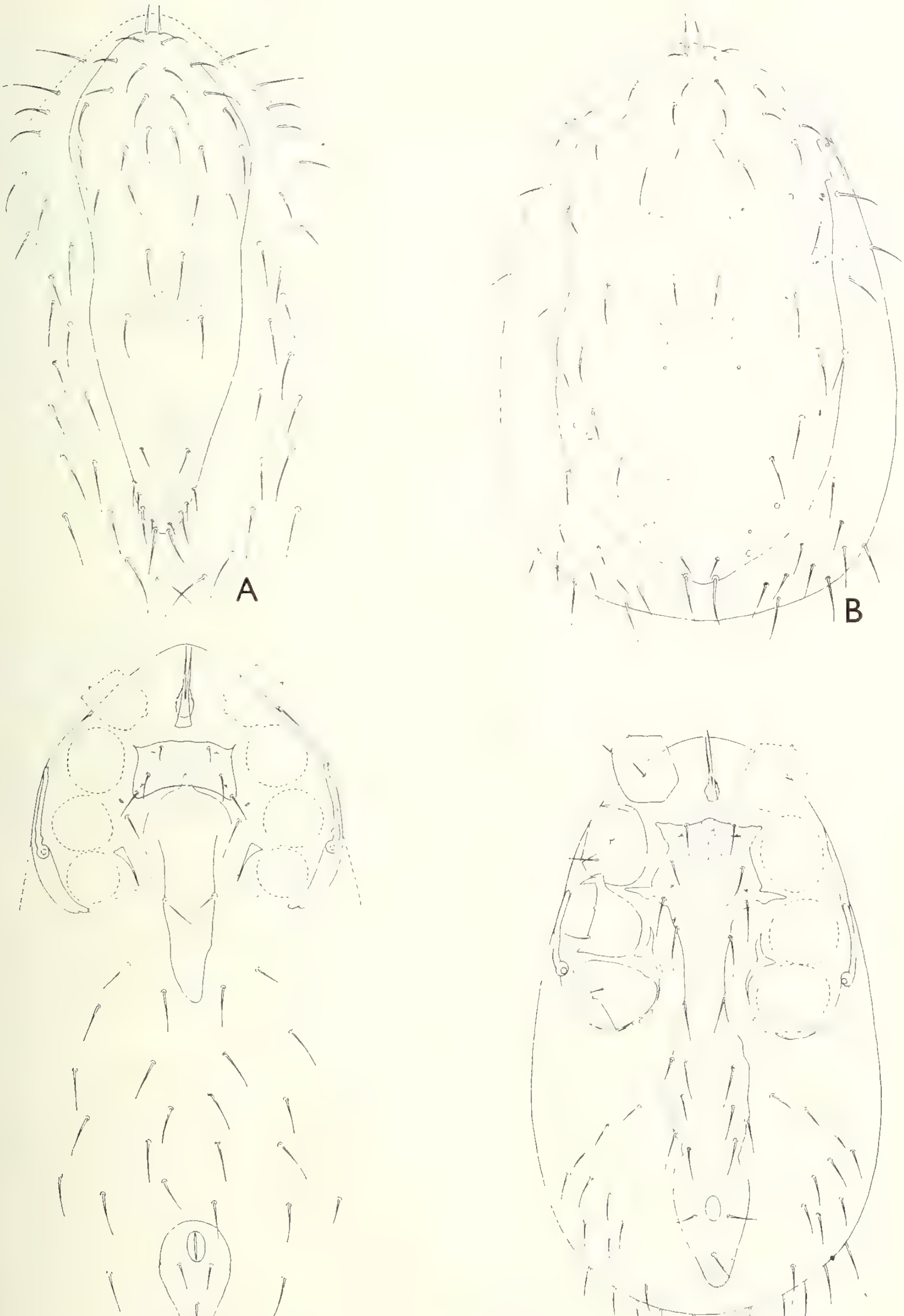
Tritosternum with denticulate hyaline border ; base 54 μ, laciniae 110 μ. Sternal shield (75 μ × 144 μ) reticulated, with three pairs of setae and two pairs of pores ; metasternals free with associated pores. Between *st*1, 87 μ ; between *st*1 and *st*3, 93 μ. Genital shield (180 μ × 90 μ) tapering, with genital setae only. Anal shield (75 μ × 63 μ) with paranal setae 18 μ, postanal seta 27 μ. Integument of opisthogaster hypertrichous (Text-fig. 85C). Peritreme extends to middle of coxa II. Anterior part of peritrematal shield extends to middle of coxa I, ending freely ; posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs normal except genu III (2—$\frac{2}{1}$, $\frac{2}{1}$—2), tibia III (2—$\frac{1}{1}$, $\frac{2}{1}$—2) and genu IV (2—$\frac{2}{1}$, $\frac{3}{1}$—1). Coxa II with prominent anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	144/54	117/66	114/66	150/60
tibia	144/51	114/63	114/60	150/54
tarsus	258/48	192/54	174/48	240/54

Male : Chelicera with segment I, 36 μ ; II, 126 μ ; movable digit edentate, 42 μ long ; spermadactyl relatively short, 54 μ from base of movable digit. Four pairs of gnathosomal setae with *c.s.* about 51 μ apart, *hyp.*2 about 39 μ apart. Deutosternum with ten denticles arranged in a single file. Corniculi membranous, internal malae leaf-like. Tectum capituli and pedipalps as in female.

FIG. 85. *Ornithonyssus pipistrelli* (Oudemans). A. Dorsal shield of female ; B. dorsum of idiosoma of male ; C. venter of idiosoma of female ; D. venter of idiosoma of male


A
B
C
D

Dorsal shield (696 μ × 360 μ) considerably broader than in the female, covering almost the entire dorsum (Text-fig. 85B) ; bearing about 25 pairs of setae. Surface of shield strongly reticulated ; unsclerotized integument of dorsum with about 12 pairs of setae.

Tritosternum with base 30 μ, laciniae 78 μ. Holoventral shield (588 μ × 123 μ) narrow, reticulated, with 19 setae excluding the anals. Between *st*1, 70 μ ; between *st*1 and *st*3, 100 μ. Paranal setae about 33 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 85D. Peritreme extends to anterior margin of coxa III ; anterior part of peritrematal shield fused with dorsal shield, posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs as in female. Coxa II with prominent anterior spine. Anterior setae on coxae II and III large and spine-like. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	120/48	96/60	99/57	132/57
tibia	126/48	84/57	93/54	126/54
tarsus	204/42	126/48	126/45	192/45

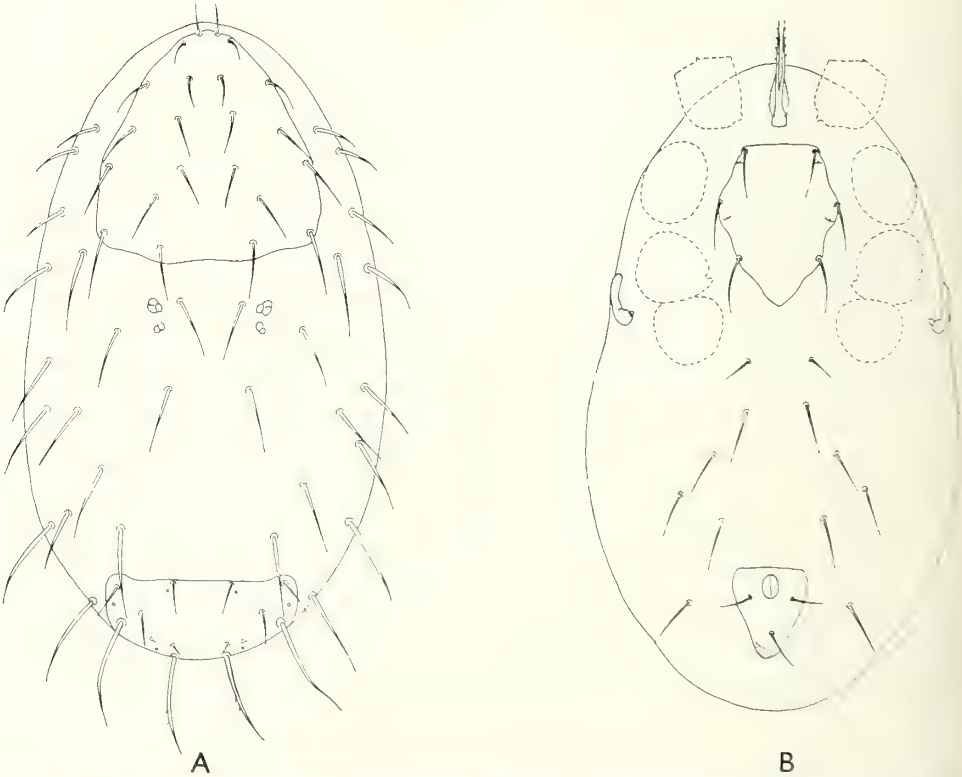


Fig. 86. *Ornithonyssus pipistrelli* (Oudemans), protonymph ; dorsum (A) and venter (B) of idiosoma.

Protonymph : Chelicera with segment I, 30 μ ; II, 99 μ ; movable digit 30 μ. Gnathosomal features essentially as in female. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.*2 about 30 μ apart. Deutosternum with nine denticles arranged in a single file. Pedipalp (1–4–5–12) with two-tined apotele ; palptrochanter with small ventral keel.

Podonotal shield (210 μ × 204 μ) with 11 pairs of setae (Text-fig. 86A) ; pygidial shield (66 μ × 180 μ) very broad, with six pairs of setae. Unsclerotized integument of dorsum with about 15 pairs of setae.

Tritosternum with base 36 μ, laciniae 45 μ. Sternal shield (150 μ × 117 μ) with three pairs of setae and two pairs of pores. Between *st*1, 66 μ ; between *st*1 and *st*3, 96 μ. Anal shield (60–63 μ × 66–69 μ) with paranal setae about 30 μ, postanal seta about 36 μ long. Opisthogaster with a pair of genital and five pairs of opisthogastric setae distributed as in Text-fig. 86B. Peritreme extends to posterior third of coxa III.

Chaetotaxy of legs normal. Length / width(in μ) of leg segments :

	I	II	III	IV
genu	63/39	54/45	48/40	60/36
tibia	63/36	54/42	51/38	60/33
tarsus	117/33	87/33	84/32	110/30

HABITAT : Found in Dorset, England, on *Eptesicus serotinus* (Schreber) and *Plecotus auritus* (Linn.). Oudemans described the species from "*Vespertilio pipistrellus*", but does not give any locality. Lange (1959) describes a closely related species (*O. pavlovskii*) from *Muscardinus avellanarius* (Linn.) in Rumania. The number and relative positions of the setae on the dorsal shield of the female appear to be identical with the condition in *O. pipistrelli.*

Genus ***STEATONYSSUS*** Kolenati

Steatonyssus Kolenati, 1858, *Wien. ent. Monatschr.* **2** : 6 ; et 1859, *S.B. Akad. Wiss. Wien.* **35** : 186.
Till & Evans, 1964, *Bull. Brit. Mus. (nat. Hist.) Zool.* **11** : 513.
Ceratonyssus Ewing, 1923, *Proc. U.S. nat. Mus.* **62** (art. 13) : 6.

Type : *Steatonyssus periblepharus* Kolenati, 1858.

Cheliceral digits edentate, lacking denticulate processes ; fixed digit with distal hyaline boss. Movable digit of male not hooked distally ; spermadactyl grooved, relatively short, a membranous lobe present between spermadactyl and digit. Pilus dentilis absent, dorsal seta minute or absent, fissures normal. Arthrodial processes absent. Chaetotaxy of venter of gnathosoma normal ; pedipalps with five free segments and a two-tined apotele ; chaetotaxy of trochanter to tibia (2–5–6–13). Palptrochanter with well-developed keel in the female. Deutosternum with six to ten denticles arranged in a single file. Corniculi membranous, internal malae simple. Tectum capituli elongate, apex fimbriated.

Dorsal sclerotization of the female comprising well-developed podonotal and opisthonotal shields. Podonotal shield with ten (*j*3 lacking), 11 or 13 pairs of setae, paraverticals (*z*1) absent. Opisthonotal shield normally with seven pairs of setae, but this number may be reduced by the absence of *J*5 or *J*5 and *Z*5. Unpaired accessory setae sometimes present in the *J* region. Lateral integument hypertrichous. Male with entire dorsal shield ; podonotal region with 11 or 12 pairs of setae ; opisthonotal region with similar chaetotaxy to the opisthonotal shield of the female, but with a tendency for the addition of *Z* and *S* setae to the shield.

Tritosternum normal, bipartite, with hyaline denticulate border. Sternal shield with three pairs of setae and two pairs of pores ; posterior margin often with a more strongly sclerotized band. Genital shield tapering posteriorly, with genital setae only. Anal shield normal. Opisthogastric cuticle usually shows hypertrichy. Metapodal shields weak. Peritrematal shields fused with podal shields of coxae IV. Male with holoventral shield.

Leg chaetotaxy typically—leg I normal, leg II normal, leg III normal except genu III ($2-\frac{2}{1}, \frac{2}{1}-2$) and tibia III ($2-\frac{1}{1}, \frac{2}{1}-2$) and leg IV normal except genu IV ($2-\frac{2}{1}, \frac{3}{1}-1$). Other exceptions occurring rarely are tibia I ($2-\frac{3}{2}, \frac{2}{1}-2$), tibia III ($2-\frac{2}{1}, \frac{2}{1}-2$) and tibia IV ($2-\frac{2}{1}, \frac{3}{1}-2$). Coxa II with strong anterior spine in both sexes.

Protonymph with dorsum of idiosoma bearing 28 (*j*2 lacking) or 29 pairs of setae. Podonotal shield with 10 or 11 pairs of setae, pygidial shield normally with four pairs. According to chaetotactic patterns of certain adults whose protonymphs have not been found, it is possible that the number of dorsal setae may be reduced to 26 (*j*2, *J*5 and *Z*5 lacking) or 28 (*J*5 missing). Venter of idiosoma with three pairs of sternal setae, one pair of genital setae and five pairs of opisthogastric setae. Anal shield normal. Gnathosoma as in female, but palptrochanter lacking ventral keel. Chaetotaxy of palps and legs normal.

KEY TO FEMALES

1 Sternal setae 1 very short, not more than one-half the length of sternal setae 2 (Text-fig. 87B) ; peritrematal shield entire anteriorly . . . **S. periblepharus** Kolenati (p. 330)

– Sternal setae 1 and 2 long, subequal in length ; anterior portion of peritrematal shield interrupted . . . . . . **S. occidentalis** Ewing (p. 334)

Steatonyssus (***Steatonyssus***) ***periblepharus*** Kolenati

Steatonyssus periblepharus Kolenati, 1858, *Wien. ent. Monatschr.* **2** : 6 ; et 1859, *S.B. Akad. Wiss. Wien* **35** : 186, pl. 8, fig. 34.

Till & Evans, 1964, *Bull. Brit. Mus. (nat. Hist.) Zool.* **11** : 562, figs. 62–67.

Female : Chelicera with segment I, 40 μ ; II, 168 μ ; movable digit 54 μ ; both digits edentate. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart, *hyp.*2 about 33 μ apart. Deutosternum with eight denticles arranged in a single file. Corniculi membranous ; internal malae simple. Tectum capituli tapering, with anterior margin fimbriated. Pedipalp (2–5–6–13) with two-tined apotele ; palptrochanter with prominent antero-ventral keel.

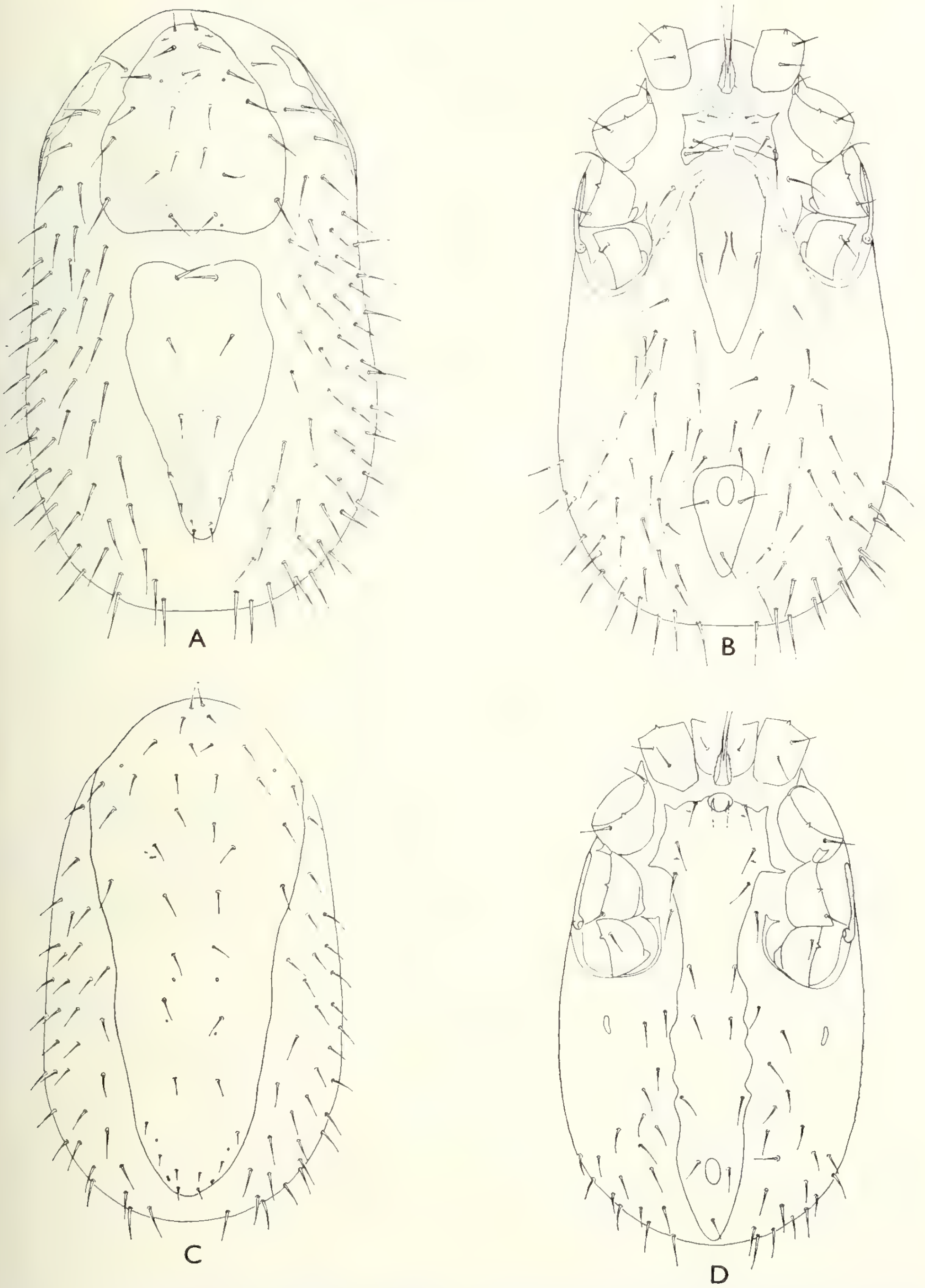


FIG. 87. *Steatonyssus periblepharus* Kolenati. A. Dorsum of idiosoma of female ; B. venter of idiosoma of female ; C. dorsum of idiosoma of male ; D. venter of idiosoma of male.

Podonotal shield (294–312 μ × 252–276 μ) bears 11 pairs of setae distributed as in Text-fig. 87A. Opisthonotal shield (348–396 μ × 180–198 μ) with seven pairs of setae. Seta *J*1 relatively stouter than the other setae on the shield. Surface of both shields reticulated ; unsclerotized integument of dorsum with numerous rather stout, spine-like setae.

Tritosternum with hyaline denticulated mambrane ; base 38 μ laciniae 102 μ. Sternal shield (45–57 μ × 130–144 μ) reticulated, not sharply demarkated from presternal area ; posterior border of shield heavily sclerotized ; bearing three pairs of setae and two pairs of pores ; metasternal setae free. Between *st*1, 45–50 μ ; between *st*1 and *st*3, 70–72 μ. Sternal seta 1 relatively short, not more than half as long as *st*2. Genital shield (144–156 μ × 75–93 μ) tapering, with genital setae only. Anal shield (114–135 μ × 80–94 μ) with par- and postanal setae subequal, about 40 μ long. Integument of opisthogaster bears numerous setae, those near the margin being relatively longer (65 μ) and stouter than the others (Text-fig. 87B). Peritreme extends to middle of coxa II ; anterior part of peritrematal shield continues to middle of coxa I ; posterior part fused with podal shields of coxa IV.

Chaetotaxy of legs normal except genu III (2—$\frac{2}{1}$, $\frac{2}{1}$—2), tibia III (2—$\frac{1}{1}$, $\frac{2}{1}$—2) and genu IV (2—$\frac{2}{1}$, $\frac{3}{1}$—1). Coxa II with prominent anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	102/54	93/69	84/60	108/54
tibia	102/48	84/60	78/54	102/48
tarsus	177/42	156/48	156/48	192/48

Male : Chelicera with segment I, 27 μ ; II, 99 μ ; movable digit 34 μ ; spermadactyl relatively short, grooved, 45 μ long from base of movable digit ; a membranous lobe is present between the spermadactyl and the digit. Fixed digit edentate with distal hyaline boss. Four pairs of gnathosomal setae with *c.s.* about 36 μ apart, *hyp.*2 about 36 μ apart. Pedipalp trochanter without ventral keel ; other features as in female.

Dorsal shield (504 μ × 228 μ) with 19 pairs of setae distributed as in Text-fig. 87C. Surface of shield reticulated. Unsclerotized integument of dorsum hypertrichous.

Tritosternum with base 21 μ, laciniae 66 μ. Holoventral shield (420 μ × 105 μ) narrow, bearing six pairs of setae excluding the anals ; metasternal setae on integument beside shield. Between *st*1, 48 μ : between *st*1 and *st*3, 75 μ. Par- and postanal setae subequal, about 24 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 87D. Peritreme extends to anterior margin of coxa III ; anterior part of peritrematal shield short, free ; posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs as in female. Anterior seta on coxa III short, spinose, with blade-like extension on proximo-anterior margin. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	75/38	66/48	50/45	72/40
tibia	75/34	54/42	50/40	69/33
tarsus	130/32	90/36	90/33	120/30

Protonymph: Chelicera with segment I, 20 μ; II, 100 μ; movable digit 30 μ. Four pairs of gnathosomal setae with *c.s.* about 33 μ apart; *hyp.2* about 27 μ apart. Pedipalp (1–4–5–12) without keel on trochanter.

Podonotal shield (180 μ × 150 μ) with 11 pairs of setae as in Text-fig. 88A; pygidial shield with four pairs of setae; unsclerotized integument of dorsum with 14 pairs of setae.

Tritosternum with base 15 μ, laciniae 60 μ. Sternal shield (140 μ × 114 μ) with three pairs of setae and two pairs of pores. Between *st*1, 60 μ; between *st*1 and *st*3, 96 μ. Anal shield (48 μ × 54–57 μ) with par- and postanal setae subequal, about 27 μ long. Integument of venter bears a pair of genital and five pairs of opisthogastric setae (Text-fig. 88B). Peritreme extends nearly to middle of coxa III.

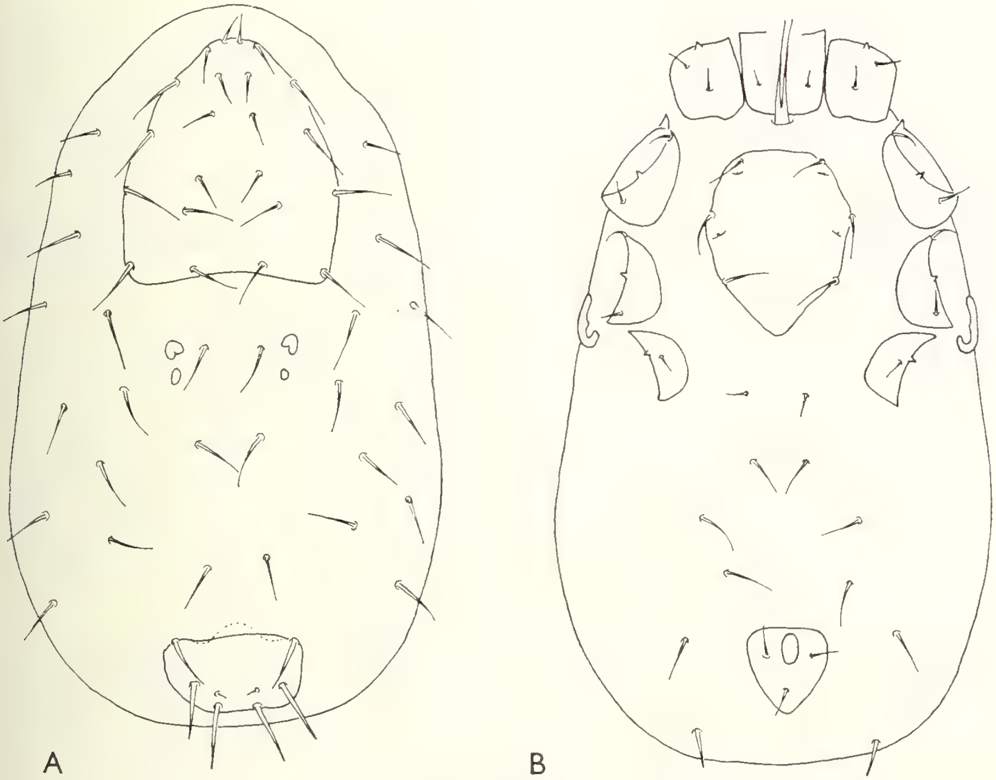


FIG. 88. *Steatonyssus periblepharus* Kolenati, protonymph; dorsum (A) and venter (B) of idiosoma.

Chaetotaxy of legs normal. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	48/40	45/42	36/39	48/36
tibia	45/34	36/39	36/36	48/33
tarsus	90/30	66/30	66/32	102/30

HABITAT : Found in Britain on *Pipistrellus pipistrellus* (Schreber) and *Myotis mystacinus* (Kuhl). Recorded from Europe, North Africa and the Near East, especially on bats of the genera *Pipistrellus* and *Myotis*.

Steatonyssus **(*Steatonyssus*)** ***occidentalis*** (Ewing)

Ceratonyssus occidentalis Ewing, 1933, *Proc. U.S. nat. Mus.* **82** (art. 30) : 10, figs.
Steatonyssus occidentalis : Radovsky & Furman, 1963, *Ann. ent. Soc. Amer.* **56** : 272, figs.
Till & Evans, 1964, *Bull. Brit. Mus.* (*nat. Hist.*) *Zool.* **11** : 559, figs.

Female : Chelicera with segment I, 27 μ ; II, 140 μ ; movable digit 40 μ ; both digits edentate. Four pairs of gnathosomal setae with *c.s.* about 45 μ apart ; *hyp.2* about 36 μ apart. Deutosternum with six denticles arranged in a single file. Corniculi membranous ; internal malae simple. Tectum capituli tapering, anterior margin weakly serrated. Pedipalp (2–5–6–13) with two-tined apotele ; palptrochanter with prominent antero-ventral keel.

Podonotal shield (288 $\mu \times$ 282 μ) with 11 pairs of setae distributed as in Text-fig. 89A ; opisthonotal shield (372 $\mu \times$ 204 μ) with seven pairs of setae. Surface of both shields reticulated, opisthonotal shield with striations posteriorly. Unsclerotized integument of dorsum hypertrichous.

Tritosternum with hyaline, denticulated membrane. Sternal shield (40 $\mu \times$ 132 μ) reticulated, with thickened posterior border ; bearing three pairs of setae and two pairs of pores ; metasternal setae free. Between *st*1, 68 μ ; between *st*1 and *st*3, 72 μ. Genital shield (144 $\mu \times$ 93 μ) tapering, with genital setae only. Anal shield (120 $\mu \times$ 96 μ) with par- and postanal setae about 40 μ long. Integument of opisthogaster hypertrichous (Text-fig. 89B). Peritreme extends to anterior margin of coxa III ; anterior part of peritrematal shield interrupted, a separate leaf-like portion lying over coxae I–II ; posterior part of peritrematal shield fused with podal elements of coxa IV.

Chaetotaxy of legs normal except genu III ($2-\frac{2}{1}, \frac{2}{0/1}-2$), tibia III ($2-\frac{1}{1}, \frac{2}{1}-2$) and genu IV ($2-\frac{2}{1}, \frac{3}{1}-1$). Coxa II with anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	96/57	84/75	72/60	102/54
tibia	96/45	78/60	75/52	102/48
tarsus	162/40	150/45	147/42	198/42

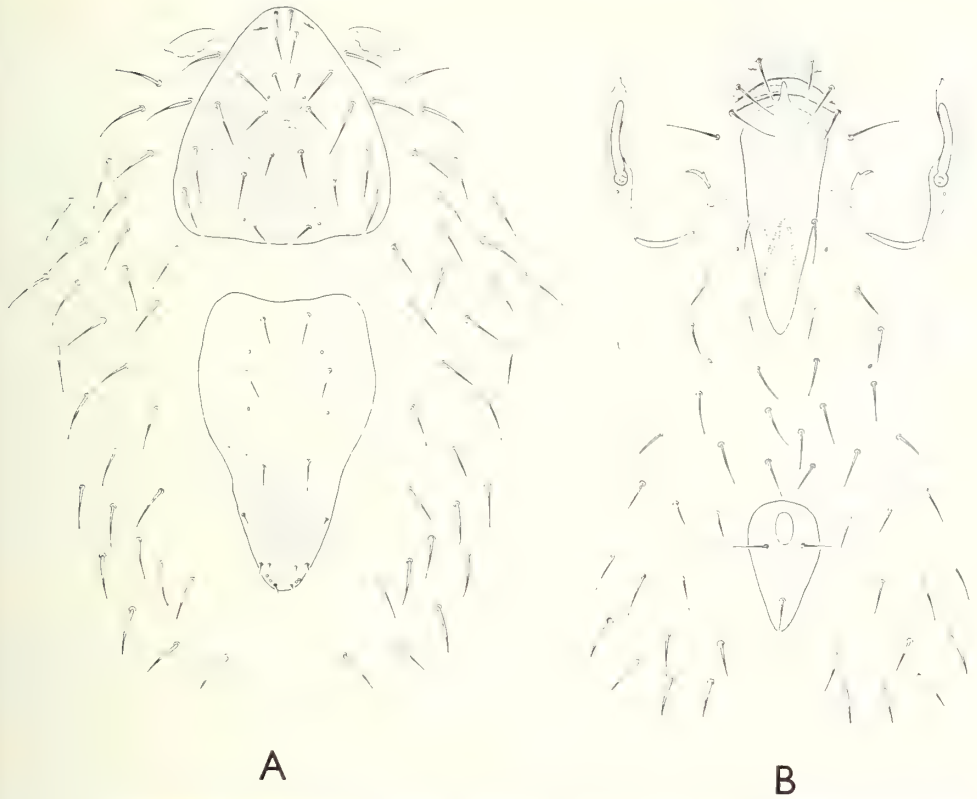


FIG. 89. *Steatonyssus occidentalis* (Ewing), female ; dorsal shields (A) ; ventral shields (B).

Male and Protonymph : Described by Radovsky & Furman (1963) and by Till & Evans (1964).

HABITAT : Found on *Eptesicus serotinus* (Schreber), Wickham Market, Suffolk, 24th June, 1964 (coll. Lord Cranbrook). This is the first record of *S.* (*S.*) *occidentalis* from Britain. Previously the species was known only from North America, where it occurs on bats of the genera *Eptesicus*, *Myotis*, *Tadarida*, *Corynorhinus* and *Lasiurus*.

Genus ***OPHIONYSSUS*** Mégnin

Ophionyssus Mégnin, 1884, *C.R. Soc. Biol. Paris* **35** : 614.
Serpenticola Ewing, 1923, *Proc. U.S. nat. Mus.* **62** (art. 13) : 6.
Sauronyssus Sambon, 1928, *Ann. trop. Med.* **22** : 106.
Neoliponyssus Ewing, 1929, *Manual of External Parasites* : 187.
Oudemansiella Fonseca, 1948, *Proc. zool. Soc. Lond.* **118** : 269.

Type : *Dermanyssus natricis* Gervais, 1844.

Cheliceral digits edentate, movable digit in the female with a well-defined hyaline flap ; fixed digit grooved, rounded anteriorly. Movable digit of male chelicera completely fused with the deeply grooved spermadactyl ; fixed digit not hooked. Dorsal seta and pilus dentilis absent ; arthrodial membrane at base of chelicera without setiform processes. Chaetotaxy of venter of gnathosoma normal, pedipalps with five free segments and a two-tined apotele. Chaetotaxy of pedipalps (2–4/5–5/6–13). Palptrochanter with a shallow, inconspicuous, weakly sclerotized keel. Deutosternum with 6–9 denticles in a single longitudinal row. Corniculi membranous, typically macronyssine. Tectum capituli elongate, obtuse, anterior margin fimbriated.

Dorsal sclerotization of the female of three basic types ; one consisting of a podonotal shield bearing nine or ten pairs of setae, two pairs of mesonotal scutellae and a small sub-circular pygidial shield normally lacking setae ; the second with a posterior extension of the podonotal shield incorporating opisthonotal setae *J*1 and *J*2, and with a discrete pygidial shield lacking setae ; the third consisting of a single dorsal shield incorporating 10 or 11 pairs of setae in the podonotal region and three pairs of *J* setae in the opisthonotal region, with setae *Z*5 on or off the shield. In the male the dorsal shield is entire, bearing 17–24 pairs of setae. Paravertical setae (*z*1) absent.

Tritosternum bipartite, with a denticulate hyaline border. Sternal shield in female with two pairs of setae and two pairs of pores, the third pair of sternal setae and the metasternals being situated on unsclerotized integument. Genital shield narrow, tapering, the genital setae placed on the integument. Anal shield pear-shaped with normal chaetotaxy. Unsclerotized integument of opisthogaster hypertrichous. Peritrematal shields fused posteriorly with podal shields of coxae IV. Metapodal and podal shields weakly developed. Male with a sternito-genital shield bearing two or three pairs of setae ; anal shield free.

Chaetotaxy of legs shows several deviations from the normal pattern : femur I (2—$\frac{5}{3}$—2), genu I and tibia I (2—$\frac{3}{2}$, $\frac{2}{1}$—2) or (2—$\frac{2}{1}$, $\frac{2}{1}$—2), femur II (1—$\frac{5}{3}$—1), genu II (2—$\frac{2}{1}$, $\frac{2}{1}$—2), tibia II (2—$\frac{1}{1}$, $\frac{2}{1}$—2), femur III (1—$\frac{3}{1}$—0), genu III (2—$\frac{2}{1}$, $\frac{2}{1}$—2), tibia III (2—$\frac{1}{1}$, $\frac{2}{1}$—2), genu IV (2—$\frac{2}{1}$, $\frac{2}{1}$—2) or (2—$\frac{2}{1}$, $\frac{3}{1}$—2) and tibia IV (2—$\frac{1}{1}$, $\frac{2}{1}$—2). Coxa II without an anterior spine. All ambulacra with a pair of claws.

Protonymph with general gnathosomal characteristics of the female. Podonotal region with 16 pairs of setae (podonotal shield with ten pairs) ; opisthonotal region with ten pairs (pygidial shield with two pairs, *J*4 and *Z*5) or 11 pairs (pygidial shield with three pairs, *J*4, *S*5 and *Z*5) of setae. Sternal shield with three pairs of setae and two pairs of pores, genital setae present. Opisthogastric cuticle with four pairs of setae. Leg chaetotaxy normal except for genu IV (1—$\frac{2}{0}$, $\frac{2}{0}$—1).

Strandtmann & Wharton (1958) recognize *Sauronyssus* as a distinct genus differing from *Ophionyssus* in the nature of the idiosomal sclerotization of the female. This appears to be the only distinguishing feature between them. The exclusion of setae *Z*5 from the entire dorsal shield of certain *Sauronyssus* suggests that a reduction of the pygidial shield also occurs between the protonymphal and adult female stages of these species and that the elongate dorsal shield may be formed by the posterior prolongation of the podonotal shield to incorporate setae *J*1, *J*3 and *J*4. In the males of both *Ophionyssus* and *Sauronyssus* on the other hand there appears to be no reduction of the pygidial shield which forms (with its protonymphal complement of setae) part of the dorsal shield. The degree of specialization of the idiosomal sclerotization exhibited by the *Ophionyssus-Sauronyssus* complex is no greater than that occurring in certain other genera of highly specialized macronyssines and dermanyssines, for example, compare *Dermanyssus gallinae* and *D. triscutatus* Krantz, and *Ornithonyssus bacoti* and *O. aridus* Furman and Radovsky. In view of this we consider *Sauronyssus* to be synonymous with *Ophionyssus*. The distinction based on the host preferences of *Ophionyssus* (snakes) and *Sauronyssus* (lizards) is not valid. *Ophionyssus monodi* (Hirst) recorded from *Acanthodactylus scutellatus* and *Ophionyssus mabuyae* Till from the skink *Mabuya striata* have the idiosomal sclerotization of the *natricis* type. In fact, the dorsal sclerotization of *O. mabuyae* is intermediate between the conditions in *O. natricis* and *O. saurarum*, having a short posterior extension of the podonotal shield which incorporates two pairs of *J* setae, but retaining a small pygidial shield.

Key to Females

1 Dorsal sclerotization consisting of a podonotal shield, two pairs of mesonotal scutellae and a pygidial shield . . . . . ***O. natricis*** (Gervais) (p. 337)
– Dorsal sclerotization consisting of a single dorsal shield 2
2 Tibia IV with two postero-dorsal setae (2—$\frac{1}{1}$, $\frac{2}{1}$—2). Dorsal shield with ten pairs of setae in the podonotal region . . . . ***O. saurarum*** (Oudemans) (p. 342)
– Tibia IV with three postero-dorsal setae (2—$\frac{1}{1}$, $\frac{3}{1}$—2). Dorsal shield with 11 pairs of setae in the podonotal region . . . . ***O. lacertinus*** (Berlese) (p. 345)

Key to Males

1 Dorsal shield with 23–24 pairs of setae. Femur III with ventral seta greatly enlarged, spur-like . . . . . . ***O. lacertinus*** (Berlese) (p. 346)
– Dorsal shield with 16–18 pairs of setae. Femur III with ventral seta normal . . 2
2 Tibia IV with three postero-dorsal setae (2—$\frac{1}{1}$, $\frac{3}{1}$—2) . ***O. natricis*** (Gervais) (p. 340)
– Tibia IV with two postero-dorsal setae (2—$\frac{1}{1}$, $\frac{2}{1}$—2) ***O. saurarum*** (Oudemans) (p. 342)

Ophionyssus natricis (Gervais)

Dermanyssus natricis Gervais, 1844, *Hist. Nat. Ins. Apt.* **3** : 223.
Ophionyssus natricis : Camin, 1953, *Chicago Acad. Sci.* no. 10 : 1, figs.
Bregetova, 1956, *Opred. Faune. SSSR.* **61** : 160, 223, figs. 556–562.
Ichoronyssus serpentium Hirst, 1915, *Proc. zool. Soc. Lond.* : 383.
?*Serpenticola easti* Ewing, 1925, *Ent. News* **36** : 18.

Female : Chelicera with segment I, 30 μ ; II, 165 μ ; movable digit 45 μ. Both digits edentate, pilus dentilis and dorsal seta absent (Text-fig. 91C). Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.2* about 42 μ apart. Deutosternum with eight or nine denticles arranged in a single file. Corniculi membranous, internal malae slender, elongated (Text-fig. 91A). Tectum capituli with anterior margin

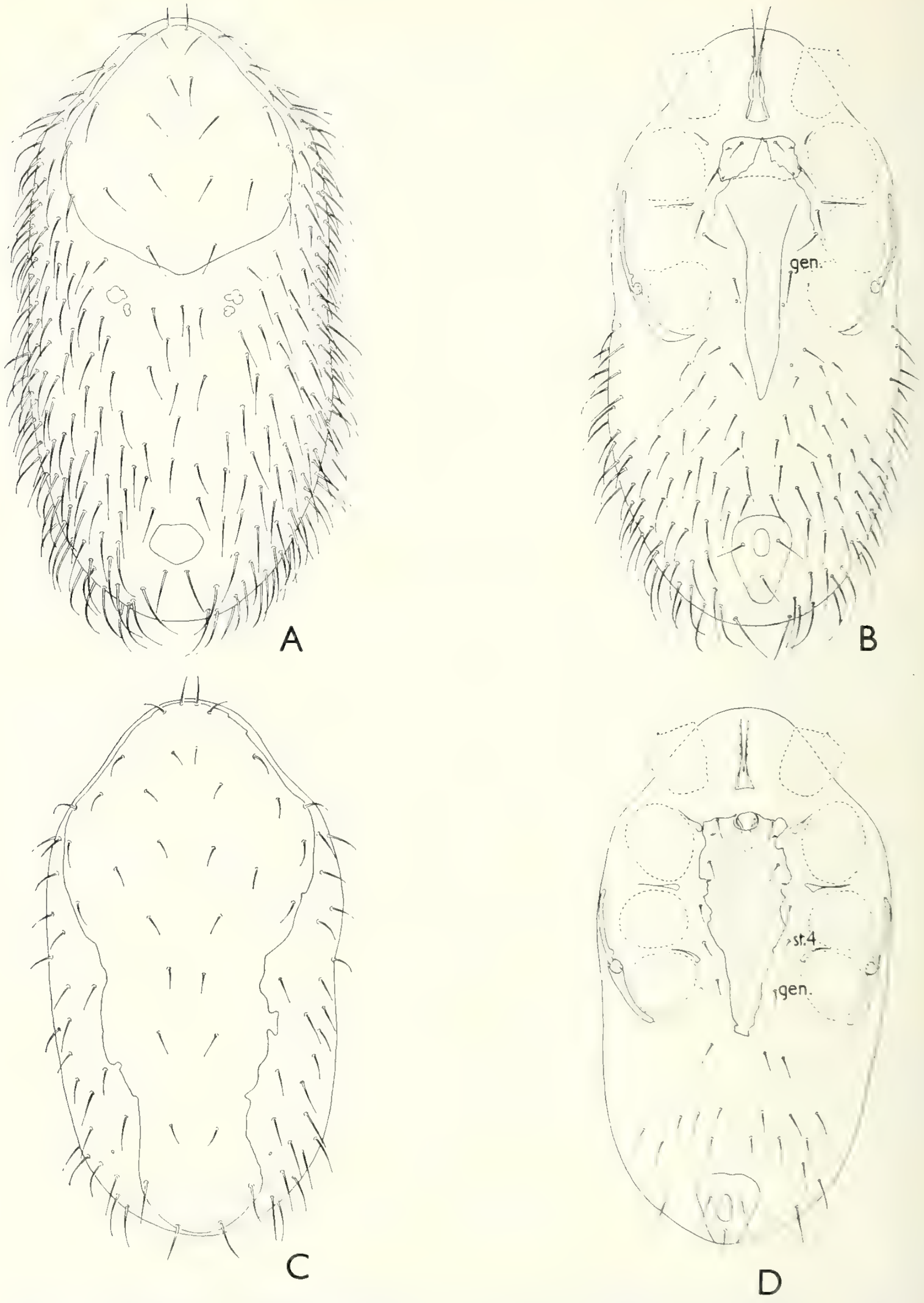


Fig. 90. *Ophionyssus natricis* (Gervais). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. dorsum of idiosoma of male; D. venter of idiosoma of male.

fimbriated. Pedipalp (2–5–6–13) with two-tined apotele ; palptrochanter with a shallow, inconspicuous, weakly sclerotized keel.

Podonotal shield (300 $\mu \times$ 276 μ) with ten pairs of setae distributed as in Text-fig. 90A ; two pairs of mesonotal scutellae lie posterior to the podonotal shield. Surface of podonotal shield granular, weakly reticulated antero-laterally. Pygidial shield (54 $\mu \times$ 45 μ) without setae. Unsclerotized integument of dorsum shows marked hypertrichy.

Tritosternum with hyaline membrane ; base 54 μ, laciniae 96 μ. Sternal shield (45 $\mu \times$ 114 μ) granular, with two pairs of setae and two pairs of pores ; the third pair of setae and the metasternals are situated on the striated integument. Between *st*1, 42 μ ; between *st*1 and *st*3, 102 μ. Genital shield (about 135 $\mu \times$ 45 μ) slender and tapering with the genital setae on the integument beside the shield. Anal shield (78 $\mu \times$ 72 μ) with paranal setae 33 μ postanal seta 36 μ long. Sclerotization and chaetotaxy of venter as in Text-fig. 90B. Peritreme extends to posterior margin of coxa II ; peritrematal shield fused posteriorly with podal elements of coxa IV.

Chaetotaxy of legs shows deviations from the normal pattern on most segments : femur I ($2-\frac{5}{3}-2$), femur II ($1-\frac{5}{3}-1$) femur III ($1-\frac{3}{1}-0$) ; genu I ($2-\frac{3}{2}, \frac{2}{1}-2$), genu III ($2-\frac{2}{1}, \frac{2}{1}-2$), genu IV ($2-\frac{2}{1}, \frac{3}{1}-2$) ; tibia I ($2-\frac{3}{2}, \frac{2}{1}-2$), tibia III ($2-\frac{1}{1}, \frac{2}{1}-2$). Coxa II without anterior spine. Length/width (in μ) of leg segments :

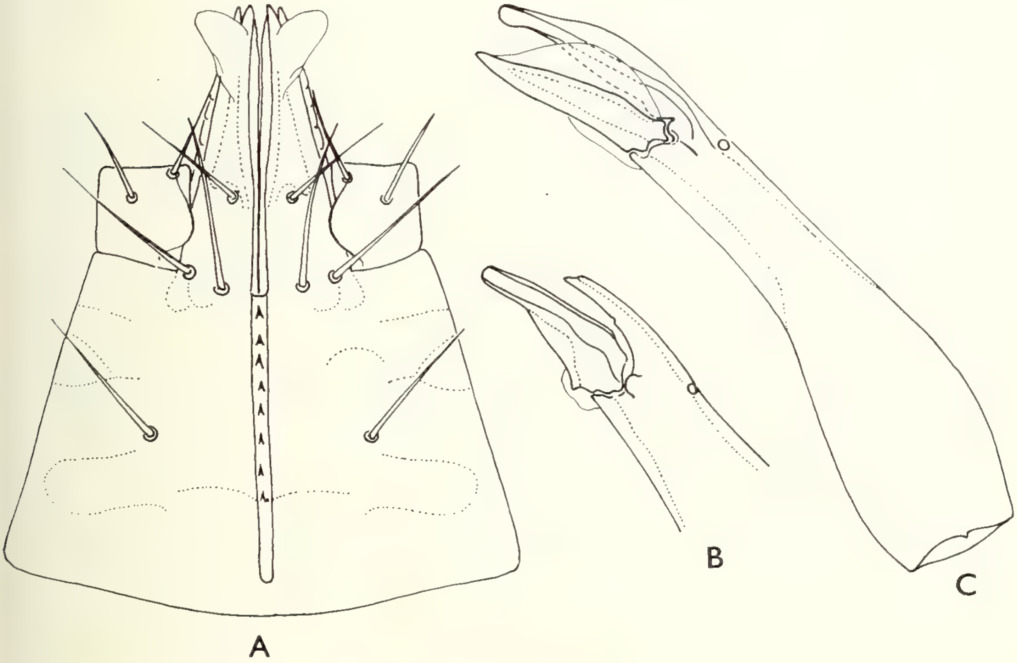


FIG. 91. *Ophionyssus natricis* (Gervais). A. Venter of gnathosoma of female ; B. chelicera of male ; C. chelicera of female.

	I	II	III	IV
genu	75/45	60/48	60/45	72/40
tibia	75/40	60/45	54/40	66/36
tarsus	123/36	96/40	90/36	110/33

Male : Chelicera with segment I, 18 μ ; II, 96 μ. Fixed digit edentate ; movable digit completely fused with grooved spermadactyl (Text-fig. 91B). Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.*2 about 36 μ apart. Other features generally as in female.

Dorsal shield (492 μ × 240 μ) with 17 pairs of setae distributed as in Text-fig. 90C. Surface of shield mainly granular with reticulations antero-laterally.

Tritosternum with hyaline membrane ; base 20 μ, laciniae 70 μ. Sternito-genital shield (204 μ × 81 μ) with *st*1 and *st*2 on the shield, *st*3, *st*4 and the genital setae on the cuticle lateral to the shield. Between *st*1, 51 μ ; between *st*1 and *st*3, 84 μ. Anal shield (66 μ × 60 μ) with par- and postanal setae about 27 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 90D. Peritreme extends to anterior margin of coxa III ; peritrematal shield fused posteriorly with podal shield of coxa IV.

Chaetotaxy of legs as in female. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	60/36	51/39	48/36	60/33
tibia	60/33	51/38	48/33	60/33
tarsus	102/33	75/30	75/30	93/30

Protonymph : Chelicera with segment I, 15 μ ; II, 110 μ ; movable digit 28 μ. Four pairs of gnathosomal setae with *c.s.* about 39μ apart, *hyp.*2 about 27 μ apart. Deutosternum with nine denticles arranged in a single file. Pedipalp (1–4–5–12) with two-tined apotele. Other gnathosomal features as in female.

Podonotal shield (204 μ × 192 μ) with eleven pairs of setae distributed as in Text-fig. 92A ; setae *s*6 and *r*2, *r*3, *r*5 and *r*6 are situated on the unsclerotized integument. Pygidial shield (63 μ × 75 μ) bears three pairs of setae.

Tritosternum with hyaline border ; base 20 μ, laciniae 75 μ. Sternal shield (110 μ × 78 μ) with three pairs of setae and two pairs of pores. Between *st*1, 48 μ ; between *st*1 and *st*3, 80 μ. Anal shield (48 μ × 48 μ) with paranal setae 21 μ, postanal seta 24 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 92B. Peritremes extend to anterior margin of coxa III.

Chaetotaxy of legs differs from the normal pattern in the presence of a postero-lateral seta on genu IV (1—$\frac{2}{0}$, $\frac{2}{0}$—1). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	42/36	42/36	40/33	48/30
tibia	48/33	42/36	36/30	48/30
tarsus	84/30	60/30	60/27	66/27

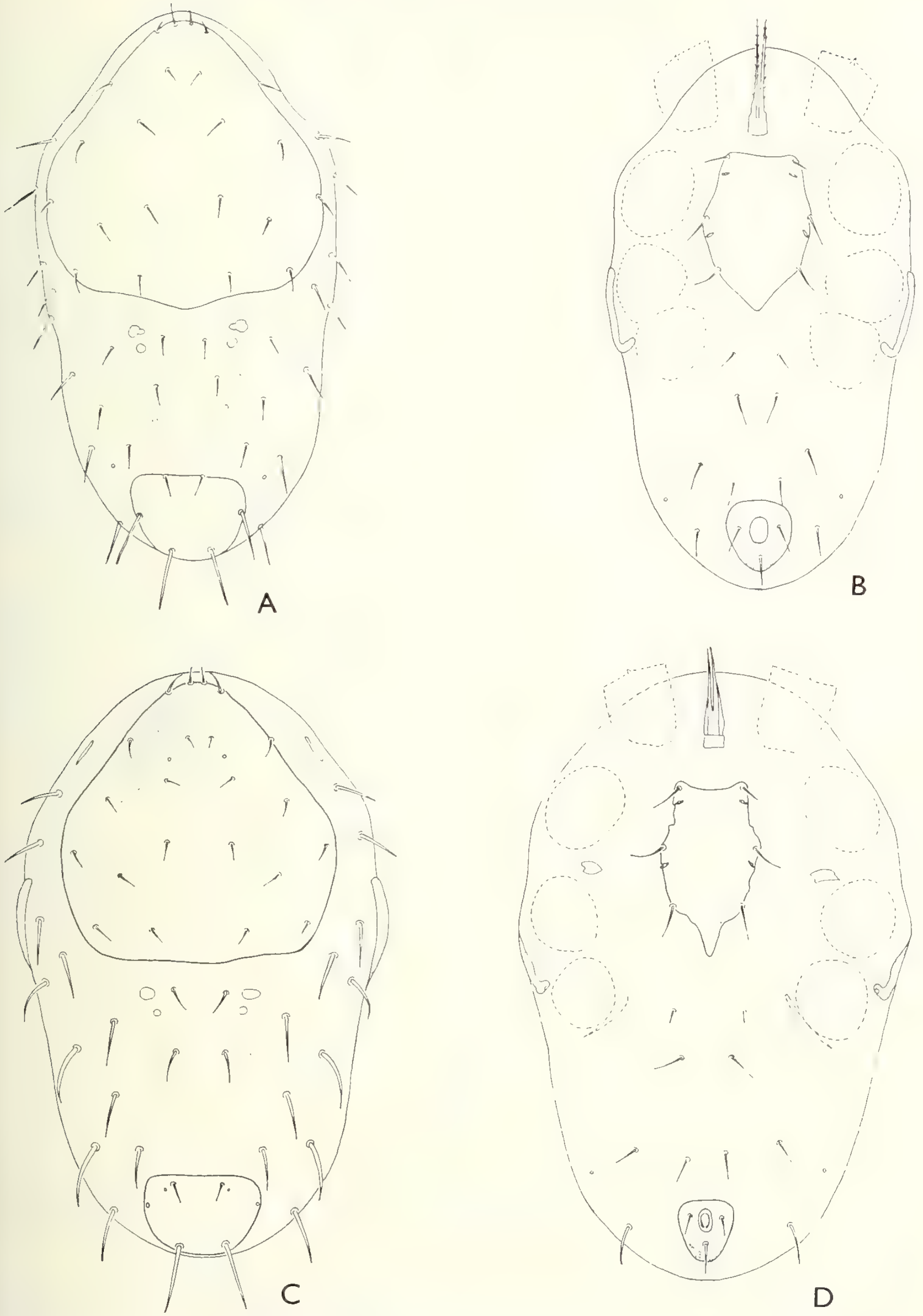


FIG. 92. A–B. *Ophionyssus natricis* (Gervais), protonymph; dorsum (A) and venter (B) of idiosoma. C–D. *Ophionyssus saurarum* (Oudemans), protonymph; dorsum (C) and venter (D) of idiosoma.

HABITAT : A common ectoparasite of snakes and lizards in vivaria all over the world. It has also been found in natural conditions on a wide variety of snakes in Africa.

Ophionyssus saurarum (Oudemans)

Liponyssus saurarum Oudemans, 1901, *Tijdschr. Ned. dierk. Vereen.* (2) **7** : 66.
Sauronyssus saurarum: Bregetova, 1956, *Opred. Faune SSSR.* **61** : 218, figs.

Female : Chelicera with segment I, 36 μ ; II, 147 μ ; movable digit 40 μ. Both digits edentate, pilus dentilis and dorsal seta absent.Four pairs of gnathosomal setae with *c.s.* about 60 μ apart, *hyp.*2 about 42 μ apart. Deutosternum with six denticles arranged in a single file. Corniculi membranous ; internal malae elongate. Tectum capituli with anterior margin fimbriated. Pedipalp (2–5–6–13) with two-tined apotele ; palptrochanter with a low ventral keel.

Dorsal shield (670 μ × 192 μ) entire, slender, bearing 13 pairs of setae distributed as in Text-fig. 93A. Surface of shield with a reticulated pattern which tends to become punctate posterior to setae *j*4. Unsclerotized integument of dorsum markedly hypertrichous.

Tritosternum with denticulate, hyaline border ; base 45 μ, laciniae 78 μ long. Sternal shield (42 μ × 120 μ) with two pairs of setae and two pairs of pores ; the third pair of setae and the metasternals are situated on unsclerotized integument. Between *st*1, 57 μ ; between *st*1 and *st*3, 96 μ. Genital shield (about 150 μ × 60 μ) tapering ; genital setae on the unsclerotized integument. Anal shield (105 μ × 75 μ) with par- and postanal setae about 33 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 93B. Peritreme extends to about anterior third of coxa II ; peritrematal shield fused posteriorly with podal elements of coxa IV.

Chaetotaxy of legs shows deviations from the normal pattern on most segments, as in *O. natricis*. In addition, tibia IV bears only three dorsal setae (2—$\frac{1}{1}$, $\frac{2}{1}$—2). Relatively stout setae are present on trochanter I (*d*), femur I (ad_1 and pd_1) and femur II (ad_1 and pd_{1-2}). Coxa II without anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	102/45	80/48	78/40	93/40
tibia	100/42	75/48	75/40	90/36
tarsus	180/36	110/40	120/36	120/36

Male: Chelicera with segment I, 20 μ ; II, 93 μ ; fixed digit edentate ; movable digit completely fused with short, grooved spermadactyl. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.*2 about 39 μ apart. Other gnathosomal features as in female.

Dorsal shield (528 μ × 264 μ) with 16 pairs of setae distributed as in Text-fig. 93C ; one or more additional unpaired setae may be situated on the margins of the podo- or

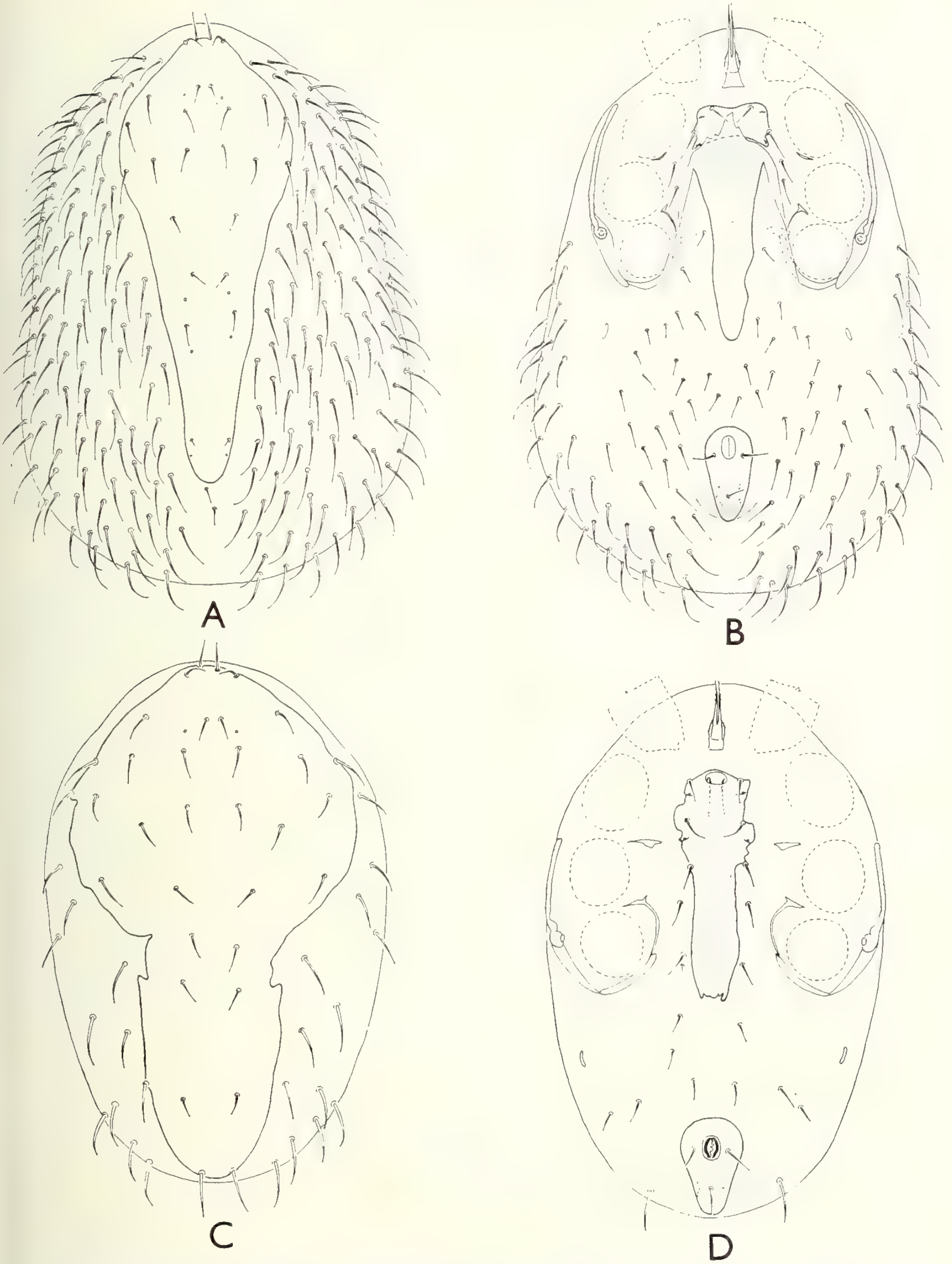


FIG. 93. *Ophionyssus saurarum* (Oudemans). A. Dorsum of idiosoma of female; B. venter of idiosoma of female; C. dorsum of idiosoma of male; D. venter of idiosoma of male.

opisthonotal regions. Surface of shield with a reticulated pattern which has a slight tendency to become punctate near the posterior tip. Unsclerotized integument of dorsum with 10 or 12 pairs of setae.

Tritosternum with base 24 μ, laciniae 48 μ. Sternito-genital shield (228 μ × 80 μ) reticulated, with three pairs of setae and two pairs of pores ; metasternal and genital setae situated on the unsclerotized integument. Anal shield (72 μ × 63 μ) with paranal setae 36 μ long, postanal seta 30 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 93D. Peritreme extends to posterior margin of coxa II ; peritrematal shield fused posteriorly with podal elements of coxa IV.

Chaetotaxy of legs as in female. Relatively stout spine-like setae present on coxae II and III, trochanter I (*d*), femora I and II (ad_1 and pd_{1-2}). Seta *v* on femora III and IV is stout basally, tapering distally. Coxa II without anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	70/40	60/45	60/40	75/40
tibia	70/36	57/42	60/40	75/40
tarsus	120/36	93/36	84/34	110/34

Protonymph : Chelicera with segment I, 20 μ ; II, 90 μ ; movable digit 24 μ. Four pairs of gnathosomal setae with *c.s.* about 38 μ apart, *hyp.*2 about 27 μ apart. Pedipalp (1–4–5–12) with two-tined apotele. Other gnathosomal features as in female.

Podonotal shield (213 μ × 180 μ) with eleven pairs of setae distributed as in Text-fig. 92C. Surface of shield reticulated. Pygidial shield (84 μ × 81 μ) bears two pairs of setae.

Tritosternum with hyaline border ; base 32 μ, laciniae 60 μ. Sternal shield (126 μ × 74 μ) with three pairs of setae and two pairs of pores ; between *st*1, 48 μ between *st*1 and *st*3, 87 μ. Anal shield (36 μ × 40 μ) with par- and postanal setae about 20 μ long. Chaetotaxy of opisthogaster as in Text-fig. 92D. Peritreme extends to anterior margin of coxa III ; peritrematal shields not developed.

Chaetotaxy of legs normal, except genu IV which has a postero-lateral seta $(1—\frac{2}{0}, \frac{2}{0}—1)$. Relatively stout setae present on the dorsal surfaces of femora I (ad_1 and pd_1), II (ad_1 and pd_{1-2}), III (ad_1) and IV (ad_{1-2}). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	48/33	42/36	45/33	57/30
tibia	54/33	45/36	45/33	57/32
tarsus	102/30	70/30	72/28	75/27

HABITAT : Recorded from lizards [*Lacerta agilis* Linn. and *L. viridis* (Laurenti)] in the Netherlands, Hungary and Italy. In Britain specimens have been obtained from *L. agilis* in Dorset, and from lizards at Albury, Surrey, and near Aberdeen, Scotland.

Ophionyssus lacertinus (Berlese)

Leiognathus lacertinus Berlese, 1892, *Acari, Myr. Scorp. Ital.* fasc. 70, no. 3, figs.

Female : Chelicera with segment I, 30 μ ; II, 180 μ ; movable digit 50 μ. Four pairs of gnathosomal setae with *c.s.* about 66 μ apart, *hyp.*2 about 38 μ apart. Deutosternum with about seven denticles arranged in a single file. Corniculi membranous ; internal malae elongated. Pedipalp (2–5–6–13) with two-tined apotele ; palptrochanter with a very shallow, inconspicuous keel.

Dorsal shield (696 μ × 264 μ) with at least 14 pairs of setae distributed as in Text-fig. 94A. There may be one or two terminal setae, or none, at the posterior tip of the shield. Surface of shield with a reticulate pattern which tends to become punctate.

Tritosternum with a hyaline border ; base 72 μ, laciniae 80 μ. Sternal shield (40 μ × 120 μ) with two pairs of setae and two pairs of pores. Between *st*1, 54 μ ; between *st*1 and *st*3, 100 μ. Genital shield (144 μ × 54 μ) tapering. Anal shield (106 μ × 84 μ) with paranal setae about 38 μ, postanal seta about 30 μ long. Peri-

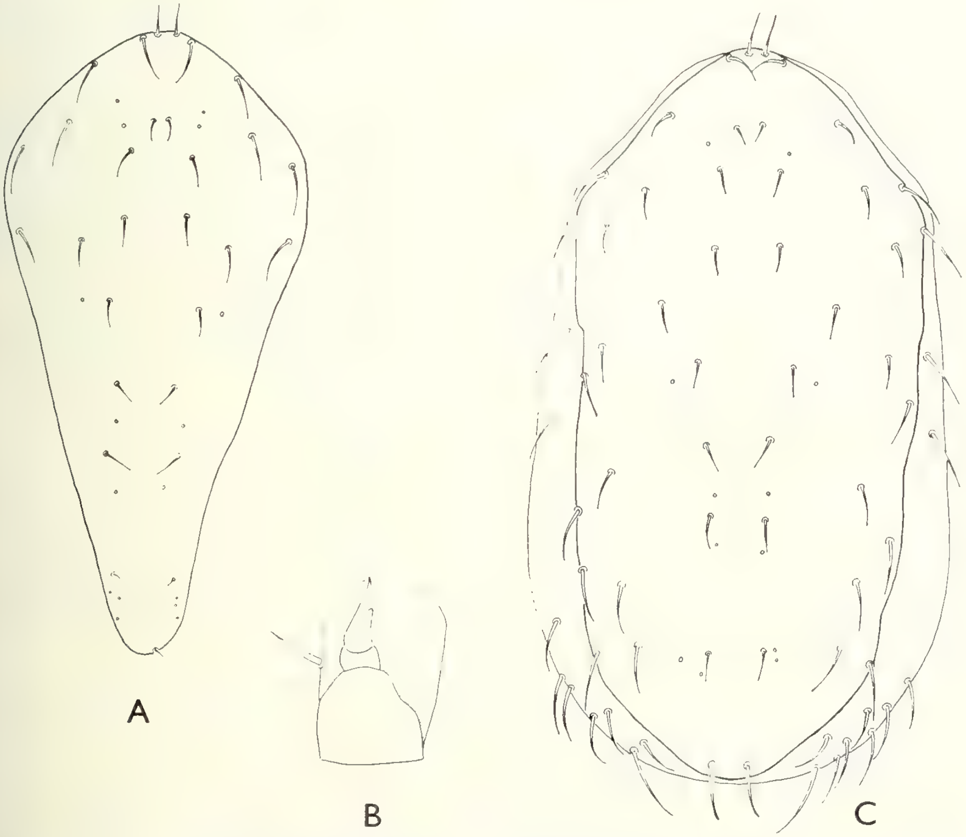


FIG. 94. *Ophionyssus lacertinus* (Berlese). A. Dorsal shield of female ; B. femur III of male, ventral view ; C. dorsum of idiosoma of male.

treme extends to anterior margin of coxa II ; peritrematal shield fused posteriorly with podal elements of coxa IV.

Chaetotaxy of legs as described for *O. natricis*. Relatively stout setae present on trochanters I, III and IV (d), femora I–II (ad_1 and pd_{1-2}), femora III–IV (ad_{1-2}). Coxa II without anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	102/45	84/51	84/48	105/42
tibia	102/40	78/48	78/42	105/39
tarsus	186/38	123/42	135/36	170/36

Male : Chelicera with segment I, 18 μ ; II, 96 μ ; fused movable digit and spermadactyl about 40 μ long. Four pairs of gnathosomal setae with *c.s.* about 40 μ apart, *hyp.*2 about 30 μ apart. Deutosternum with eight denticles arranged in a single file. Other gnathosomal features as in female.

Dorsal shield (516 μ × 250 μ) broader than in female, with 13 pairs of setae distributed as in Text-fig. 94C ; one or more additional unpaired setae may be present on the margin of the opisthonotal region. Unsclerotized integument of dorsum with nine or ten pairs of setae.

Tritosternum with base 20 μ, laciniae 54 μ. Sternito-genital shield (216 μ × 75 μ) reticulated, with *st*1 and *st*2 on the shield, *st*3, *st*4 and genital setae on the unsclerotized integument. Between *st*1, 45 μ ; between *st*1 and *st*3, 90 μ. Anal shield (60 μ × 57 μ) with paranal setae 36 μ, postanal seta 30 μ long. Opisthogaster with about seven pairs of setae. Peritreme extends to posterior margin of coxa II ; peritrematal shield fused posteriorly with podal elements of coxa IV.

Chaetotaxy of legs and setal form as in female. In addition, coxa III bears a relatively stout anterior seta and femur III has a greatly enlarged, spur-like ventral seta (Text-fig. 94B). Length/width (in μ) of leg segments :

	I	II	III	IV
genu	66/38	60/40	60/42	70/36
tibia	70/36	57/40	60/40	72/34
tarsus	117/32	80/33	96/33	105/30

HABITAT : Parasitic on *Lacerta muralis* (Laurenti) in Italy and on *Lacerta viridis* (Laurenti) imported into Britain from Italy.

Subfamily **DERMANYSSINAE** Kolenati

Dermanyssidae Kolenati, 1859, *S.B. Akad. Wiss. Wien* **35** : 171.

Adults : Chelicerae of female strongly modified, resembling stylets ; second segment enormously elongated, slender ; digits minute, weakly dentate. Pilus dentilis, dorsal seta and arthrodial processes absent. Male chelicera with second segment normal in length, spermadactyl long and entirely fused with the movable digit; fixed digit slender, usually shorter than the spermadactyl, rarely equal in length. Chaetotaxy of venter of gnathosoma normal. Pedipalps with five free segments, apotele two-tined; chaetotaxy of trochanter to tibia (2–5–6–14) in *Liponyssoides* and some *Dermanyssus*, but showing deficiency on femur and tibia, rarely genu, in most *Dermanyssus*. Palptrochanter without medio-ventral keel. Deutosternum with nine or more denticles in a single file. Hypostome compact, elongate; corniculi never horn-like, usually membranous; internal malae small, simple. Tectum capituli in the form of a triangular lobe.

Dorsum of idiosoma of female with reduced sclerotization comprising an entire shield formed by the posterior extension of the podonotal shield; mesonotal scutellae sometimes present; small pygidial shield retained in some *Liponyssoides*. Male with entire dorsal shield. Primary chaetotaxy of the dorsum of the idiosoma showing hypotrichy, paravertical seta (*z*1) absent, dorsal series (*J*) often reduced. Hypertrichy of lateral and marginal series and of the opisthogaster apparent in some species, particularly *Liponyssoides*. Dorsal setae simple.

Tritosternum well developed, biramous, laciniae smooth or pilose; denticulate hyaline margin present or absent. Sternal shield in the female with two, rarely three, pairs of setae and two pairs of pores; metasternal setae present or absent. Genital shield broadly rounded or tapering posteriorly and bearing one pair of genital setae. Anal shield normal, aciculated area conspicuous; no euanal setae. Metapodal shields small, inconspicuous. Peritrematal shield fused with the podal shields posterior to coxae IV; peritremes variable in length. Podal shields weakly developed. Male with holoventral shield, or sternito-genital and ventro-anal shields, or sternito-genital and anal shields. Genital orifice presternal.

All legs six-segmented with well developed ambulacra. Segmental chaetotaxy extremely diverse and often showing intraspecific variation. Tarsi III and IV in male with seta pv_2 modified into a short, tooth-like projection. Coxae II–IV without sclerotized ridges. Anterior spine of coxa II usually absent, present in some *Liponyssoides*.

Larva: Relatively inactive, non-feeding instar. Chelicerae without elongated second segment; digits minute, edentate, lacking setae, fissures and arthrodial processes. Pedipalps in *Dermanyssus* apparently four-segmented (tibia and tarsus fused), chaetotaxy of basal three segments (0–4–5). Hypostome with two pairs of setae; corniculi and internal malae degenerate; deutosternal denticles weak or absent. Idiosoma without distinct sclerotization. Podonotal region with seven to nine pairs of short setae, opisthonotal region with variable number of microsetae, *J*5 always present. Tritosternum biramous, relatively small. Sternal region with three pairs of setae, opisthogastric region with two pairs of setae excluding the normal three setae associated with the non-functional anus. Stigmata and peritremes absent. Leg chaetotaxy normal for this instar.

Larval stage known only for a few species.

Protonymph : Active, feeding instar. Chelicerae, basis-capituli and hypostome as in the female. Pedipalpal chaetotaxy (1–4–5–12), rarely genu and tibia deficient ; palptrochanter without medio-ventral keel.

Dorsal sclerotization comprising well developed podonotal shield with marked posterior extension ; mesonotal scutellae conspicuous, pygidial shield minute, bearing at the most one pair of setae, or represented by small scutellae or absent. Podonotal shield with 7–11 pairs of setae. Opisthonotum with four or five pairs of setae in the *J* series, never markedly hypertrichous. Tritosternum as in female. Intercoxal region with three pairs of sternal setae on a distinct sternal shield ; genital setae present (*Liponyssoides*) or suppressed (*Dermanyssus*). Opisthogastric cuticle with six pairs of setae. Anal shield well-defined and with normal three setae. Stigmata and short peritremes present. Chaetotaxy of legs normal for this instar.

Deutonymph : Active feeding instar. Gnathosoma, dorsal sclerotization and chaetotaxy as in the female. Tritosternum biramous, laciniae long, smooth or pilose. Sternito-genital shield well sclerotized and normally bearing four pairs of sternal setae, rarely three pairs due to the suppression of the metasternals ; genital setae present, on or flanking the posterior extremity of the sternito-genital shield. Chaetotaxy of opisthogaster as in female ; anal shield well developed and with three setae. Metapodal shields small, stigmata and peritremes as in female. Leg chaetotaxy as in corresponding adults.

Genus **DERMANYSSUS** De Geer

Dermanyssus De Geer, 1778, *Mém. Hist. Ins.* **7** : 106.

Type : *Acarus gallinae* De Geer, 1778.

Chelicerae of female resembling stylets, second segment greatly elongated, digits minute, weakly dentate. Pilus dentilis, dorsal seta and arthrodial processes absent. Male chelicera with segments normal in size, fixed digit reduced, spermadactyl long, grooved, completely fused with movable digit. Chaetotaxy of venter of gnathosoma normal ; pedipalp with five free segments and a two-tined apotele. Chaetotaxy of palptrochanter to tibia normal (2–5–6–14) in some *Dermanyssus*, but usually showing deficiency on the femur and tibia (2–4–6–12) and occasionally also on the genu (2–4–5–7/8). Deutosternum with nine or more denticles in single file. Hypostome elongate, corniculi membranous ; internal malae small, simple ; tectum capituli elongate, triangular, with smooth margin.

Dorsal shield in female entire but reduced, mesonotal scutellae sometimes present ; podonotal region of shield with 7 to 11 pairs of setae (setae *j3* and *z1* absent) ; opisthonotal region with from one to four pairs of setae. Male with entire dorsal shield incorporating a greater number of setae than in the female, usually 18–20 pairs (13–14 pairs in the podonotal and 5–6 pairs in the opisthonotal region).

Tritosternum normal, bipartite, with denticulate, hyaline margin. Sternal shield usually with two pairs of setae and one or two pairs of pores ; metasternal setae present or absent. Genital shield with genital setae only ; anal shield with normal chaetotaxy ; metapodal shields inconspicuous. Chaetotaxy of opisthogastric cuticle variable. Peritremes variable in length ; peritrematal shields fused with podal shields posterior to coxae IV. Male with holoventral shield, or with sternitogenital and ventro-anal shields.

In most species the segmental chaetotaxy of the legs shows deviations from the normal complement and protonymphal patterns are often retained, especially on tibiae II–IV. Intraspecific variation is not uncommon. The *ad* and *pd* series on tibia I each comprises only two setae, and the *ad* series on tibia IV and *pd* series on genu IV also only two setae. Tarsi III and IV in male with seta pv_2 modified to form a tooth-like projection. Ambulacra and claws well developed, coxa II without anterior spine.

Immature stages have the features described in the diagnosis of the subfamily.

KEY TO FEMALES

1 Dorsal shield with at least eight pairs of setae in the podonotal region (*j4* present) ; no conspicuous pore on shield posterior to seta *s4*. Palptibia with 12 setae. Metasternal setae usually present 2

– Dorsal shield with seven pairs of setae in the podonotal region (*j4* absent) ; a conspicuous pore present on each side of the shield posterior to seta *s4*. Palptibia with 7 or 8 setae. Metasternal setae absent . . . **D. alaudae** (Schrank) (p. 359)

2 Dorsal shield with four pairs of setae in *J* series (*J2* present) ; with 9 or 11 pairs of setae in podonotal region (setae *z6* present) 3

– Dorsal shield with three pairs of setae in *J* series (*J2* absent) ; with eight pairs of setae in podonotal region (*z6* absent or on unsclerotized cuticle) 4

3 Peritreme extends at least to middle of coxa II. Setae *j1* and *s1* situated on the dorsal shield. Genu IV with one postero-lateral setae **D. gallinae** (De Geer) (p. 350)

– Peritreme extends to middle of coxa III. Setae *j1* and *s1* off the dorsal shield. Genu IV with two postero-lateral setae . **D. chelidonis** Oudemans (p. 353)

4 Opisthogaster with arc of stout, spine-like setae. Anal shield with maximum width about one and one-half times its length to base of postanal seta. Setae *z2* and *z4* on dorsal shield considerably longer than seta *j4*. Tibia I with two ventral setae **D. quintus** Vitzthum (p. 361)

– Opisthogaster without arc of stout spines. Anal shield with maximum width approximately equal to its length. Setae *z2*, *z4* and *j4* on dorsal shield subequal. Tibia I with three ventral setae . . . **D. hirundinis** (Hermann) (p. 356)

KEY TO PROTONYMPHS[10]

1 Podonotal shield with nine pairs of setae, *j1* on the shield ; opisthonotal region of dorsum with *J* series complete (*J1–J5*) 2

– Podonotal shield with seven or eight pairs of setae, *j1* off the shield ; opisthonotal region of dorsum with setae *J2* lacking 3

2 Posterior extension of podonotal shield relatively short, rounded, reaching level of setae *J1* (Text-fig. 97A) . . . . . . **D. gallinae** (De Geer) (p. 353)

– Posterior extension of podonotal shield relatively long, pointed, extending beyond level of setae *J2* (Text-fig. 97B) . . . . **D. chelidonis** Oudemans (p. 356)

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[10] Protonymph of *D. quintus* Vitzthum not known.

3 Podonotal shield with eight pairs of setae (*j*4 present) ; palptibia with 12 setae **D. hirundinis** (Hermann) (p. 358)

– Podonotal shield with seven pairs of setae (*j*4 absent) ; palptibia with eight setae **D. alaudae** (Schrank) (p. 360)

Dermanyssus gallinae (De Geer)

Acarus gallinae De Geer, 1778, *Mém. Hist. Ins.* **7** : 111.
Dermanyssus gallinae: Evans & Till, 1962, *Ann. Mag. nat. Hist.* (13) **5** : 283.
Dermanyssus avium Dugès, 1834, *Ann. Sci. nat. zool.* (2) **1** : 18.
Dermanyssus evotomydis Ewing, 1933, *Proc. U.S. nat. Mus.* **82** (art. 30) : 11.

[For detailed synonymy see Oudemans (1936), p. 299.]

Female : Chelicera with segment I, 45 μ ; II, approximately 276 μ ; digits minute, weakly dentate (Text-fig. 96C). Four pairs of gnathosomal setae with *c.s.* about 57 μ apart ; *hyp*.2 about 45 μ apart ; *hyp*.1 relatively stout. Deutosternum with 11 denticles arranged in single file. Corniculi membranous, with sclerotized bars (Text-fig. 96B). Tectum capituli elongate, triangular, with smooth margin. Pedipalp (2–4–6–12) with two-tined apotele.

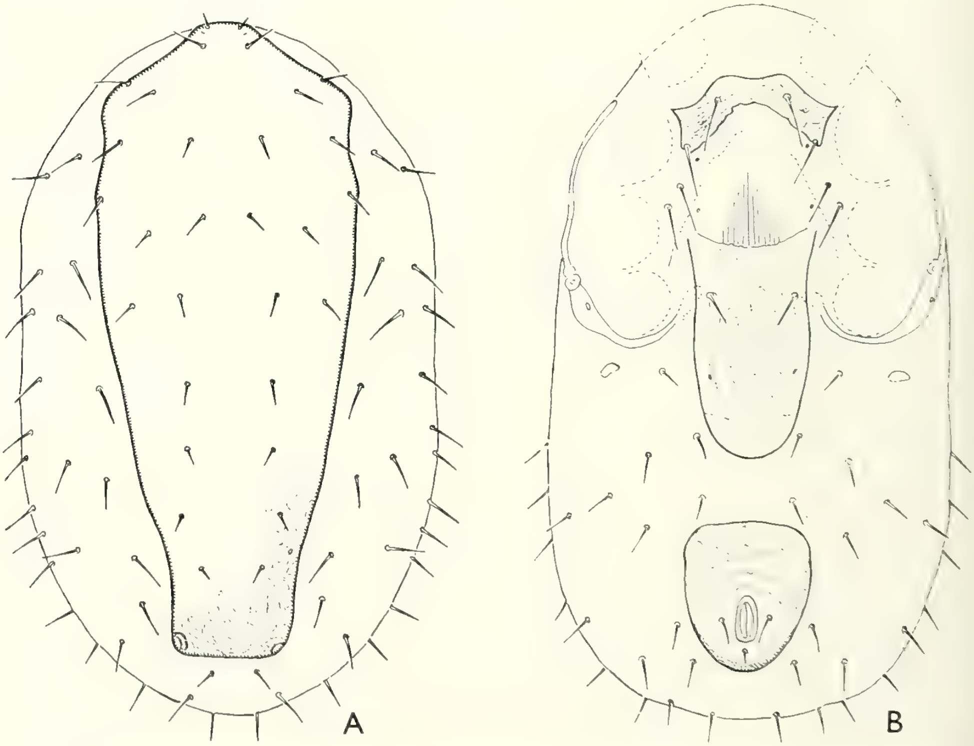

FIG. 95. *Dermanyssus gallinae* (De Geer), female ; dorsum (A) and venter (B) of idiosoma.

Dorsal shield (756 μ × 300 μ) with 15 pairs of setae distributed as in Text-fig. 95A; setae *J5* situated posterior to the shield; setae *J3* and *J4* sometimes asymmetrically arranged; *J3* may be unpaired. Surface of shield reticulated.

Tritosternum biramous, with denticulate, hyaline margin. Sternal shield (24 μ × 150 μ) reticulated, with two pairs of setae and one pair of pores; setae *st3*, metasternal setae and two pairs of pores situated on the unsclerotized cuticle. Between *st1*, 78 μ; between *st1* and *st3*, 88 μ. Genital shield (198 μ × 126 μ) reticulated; with genital setae only. Anal shield (140 μ × 123 μ; maximum width 150 μ) with paranal setae 36 μ long, postanal seta 20 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 95B. Peritreme extends to anterior half of coxa II; peritrematal shield fused posteriorly with podal elements of coxae IV.

Chaetotaxy of legs shows deviations from the normal on most segments, the protonymphal patterns being retained on femur III and tibiae II–IV:

	I	II	III	IV
femur	$2-\frac{5}{3/4}-2$	$2-\frac{5}{3}-1$	$1-\frac{3}{1}-0$	$1-\frac{3}{1}-1$
genu	$2-\frac{3}{2}, \frac{2}{1}-2$	$2-\frac{2}{1}, \frac{2}{1}-2$	$2-\frac{2}{1}, \frac{2}{0}-2$	$2-\frac{2}{1}, \frac{2}{0}-1$
tibia	$2-\frac{2}{2}, \frac{2}{1}-2$	$1-\frac{1}{1}, \frac{2}{1}-1$	$1-\frac{1}{1}, \frac{2}{1}-1$	$1-\frac{1}{1}, \frac{2}{1}-1$

Coxa II without anterior spine. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	114/66	96/60	84/54	108/54
tibia	108/60	90/57	84/52	102/48
tarsus	186/48	150/45	150/42	192/42

Male: Chelicera with segment I, 54 μ; II, 84 μ; fixed digit reduced, spermadactyl long (105 μ), grooved, completely fused with movable digit (Text-fig. 96D). Four pairs of gnathosomal setae with *c.s.* about 50 μ apart; *hyp.2* about 45 μ apart; *hyp.1* normal. Other gnathosomal features as in female.

Dorsal shield (636 μ × 276 μ) relatively broader than in the female, bearing 19 or 20 pairs of setae; three additional pairs (*s3*, *r3* and *s5*) in the podonotal and one pair (*J5*) in the opisthonotal region; in some specimens *Z1* is also on the shield.

Tritosternum with hyaline denticulate margin. Holoventral shield (528 μ × 126 μ) with five pairs of setae in the sternito-genital region, two pairs in the ventral region and the usual three anal setae; sometimes one or more additional opisthogastric setae may be incorporated. Between *st1*, 63 μ; between *st1* and *st3*, 110 μ; paranal setae 27 μ, postanal seta 18 μ long. Peritreme extends to anterior margin of coxa II; peritrematal shield fused anteriorly with dorsal shield and posteriorly with podal elements of coxa IV. Unsclerotized cuticle of opisthogaster with six pairs of setae (Text-fig. 96A).

Chaetotaxy of legs as in female; seta pv_2 on tarsi III and IV modified to form a backwardly directed tooth-like projection (Text-fig. 96E). Coxa II without anterior spine. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	87/54	72/48	66/45	81/45
tibia	90/50	70/45	72/42	87/42
tarsus	126/42	102/40	108/36	135/36

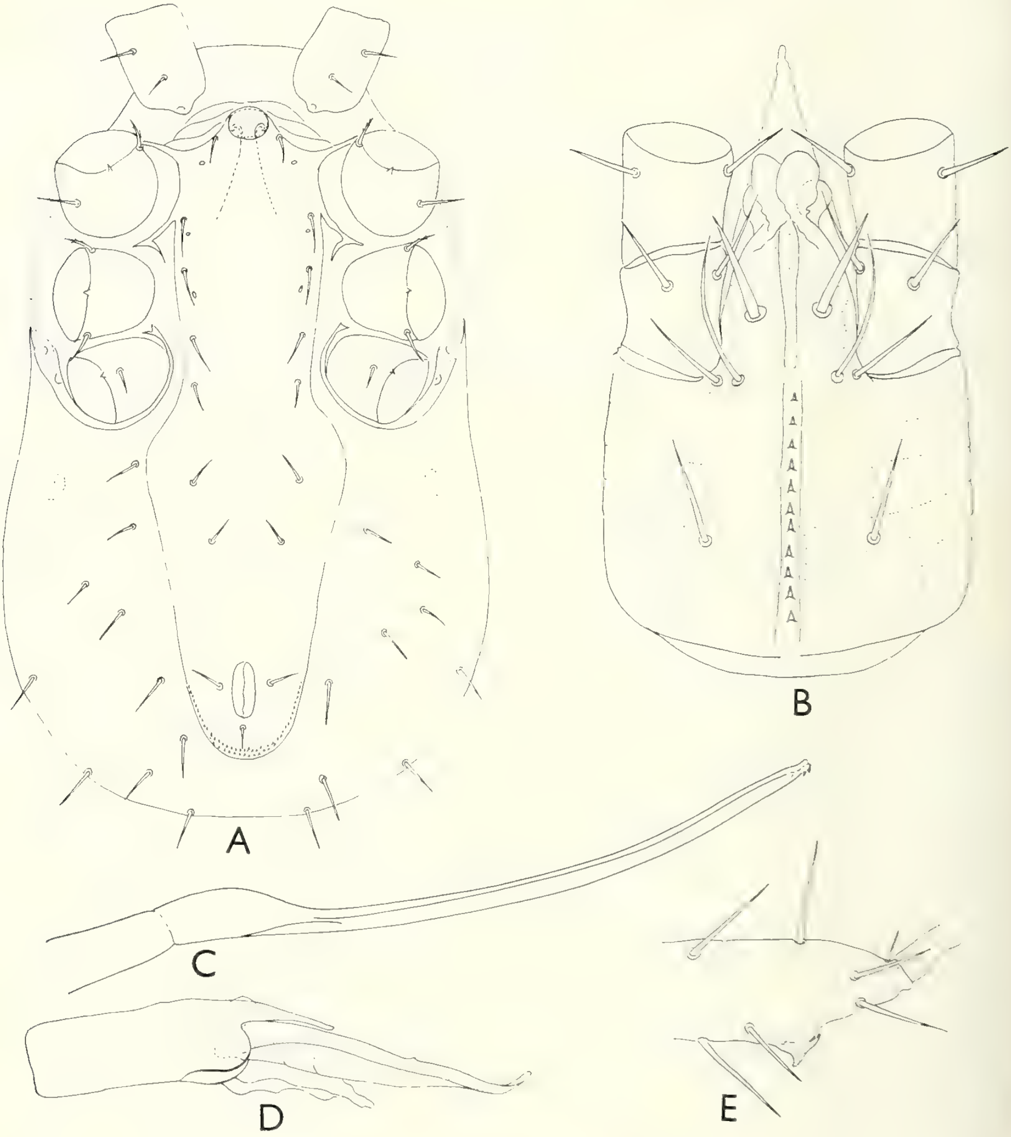

Fig. 96. *Dermanyssus gallinae* (De Geer). A. Venter of idiosoma of male; B. venter of gnathosoma of female; C. chelicera of female; D. chelicera of male; E. distal half of tarsus IV of male.

Protonymph : Gnathosoma, excluding pedipalps, essentially as in the female, but not so well developed. Four pairs of gnathosomal setae with *c.s.* about 36 μ apart, *hyp*.2 about 33 μ apart. Pedipalps with normal chaetotaxy (1–4–5–12) for this instar.

Podonotal shield (276 μ × 120 μ ; maximum width 204 μ) with a short posterior prolongation as in Text-fig. 97A ; bearing nine pairs of setae. Opisthonotal region of dorsum with *J* series complete.

Tritosternum with base 45 μ, laciniae 70 μ. Sternal shield (168 μ × 108 μ) with three pairs of setae and two pairs of pores. Between *st*1, 50 μ ; between *st*1 and *st*3, 120 μ. Genital setae absent. Anal shield (66 μ × 66 μ ; maximum width 75 μ) with paranal setae 15 μ, postanal seta about 6 μ long. Opisthogastric cuticle with six pairs of setae. Peritreme extends to middle of coxa III.

Chaetotaxy of legs normal for this instar except tibia IV which sometimes lacks the postero-lateral seta $(1—\frac{1}{1}, \frac{2}{1}—0/1)$. Coxa II without anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	60/48	50/40	42/36	56/36
tibia	63/42	50/38	42/34	60/36
tarsus	114/36	96/30	96/30	130/30

HABITAT : *D. gallinae* is primarily an avian parasite of world-wide distribution which will attack mammals in the absence of its normal host. The hosts most commonly recorded are domestic fowl, turkey, duck, pigeon (*Columba livia* Gmelin), English sparrow [*Passer domesticus* (Linn.)], starling (*Sturnus vulgaris* Linn.) and canaries [*Serinus canarius* (Linn.)].

Dermanyssus chelidonis Oudemans

Dermanyssus hirundinis: Berlese, 1889, *Acar., Myr. Scorp. ital.* fasc. 53, no. 3.

Dermanyssus chelidonis Oudemans, 1939, *Zool. Anz.* **126** : 306 (nom. nov. pro *D. hirundinis* Berlese, 1889, non Hermann, 1804).

Dermanyssus chelidonis: Evans & Till, 1962, *Ann. Mag. nat. Hist.* (13) **5** : 283.

Female : Chelicera with segment I, 60 μ ; II, 420 μ ; digits minute (about 6 μ), weakly dentate. Four pairs of gnathosomal setae with *c.s.* about 70 μ apart, *hyp*.2 about 57 μ apart ; *hyp*.1 relatively stout. Deutosternum with 12 denticles in a single file. Corniculi membranous. Tectum capituli elongate, triangular, with smooth margin. Pedipalp (2–4–6–12) with two-tined apotele.

Dorsal shield (816 μ × 372 μ) with 13 pairs of setae distributed as in Text-fig. 98A ; setae *j*1 and *J*5 off the shield. Surface of shield patterned as in Text-fig. 98A.

Tritosternum with denticulate hyaline margin. Sternal shield (45 μ × 150 μ) with two pairs of setae and two pairs of pores ; *st*3 and metasternals free on un-

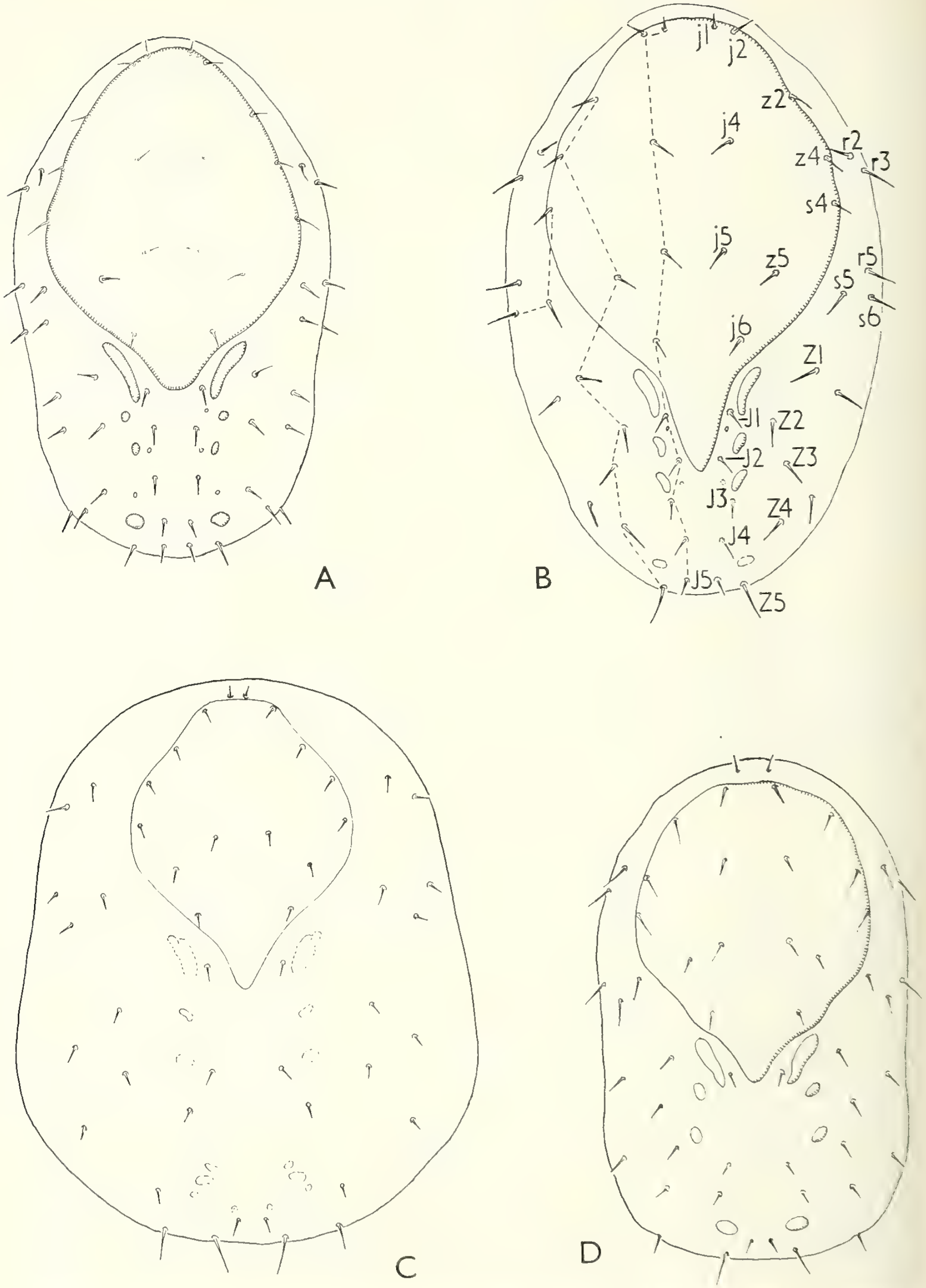
j1
j2
z2
j4
z4
r2
r3
s4
j5
z5
r5
s5
s6
j6
Z1
J1
Z2
J2
Z3
J3
Z4
J4
J5
Z5
A
B
C
D

Fig. 97. Dorsum of idiosoma of protonymphs of four species of *Dermanyssus*; *D. gallinae* (A); *D. chelidonis* (B); *D. alaudae* (C); *D. hirundinis* (D).

sclerotized cuticle. Between *st*1, 100 μ ; between *st*1 and *st*3, 93 μ. Genital shield (222 μ × 144 μ) with genital setae only. Anal shield (168–174 μ × 150 μ ; maximum width 180–210 μ) with paranal setae 40 μ, postanal seta 27 μ. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 98B. Peritreme extends to anterior half of coxa III ; peritrematal shield short and free anteriorly, posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs with deviations from the normal pattern affecting most segments, with retention of the protonymphal pattern on femur III and tibiae II–IV :

	I	II	III	IV
femur	$2-\frac{5}{3}-2$	$2-\frac{5}{3}-1$	$1-\frac{3}{1}-0$	$0-\frac{3}{2}-1$
genu	$2-\frac{3}{2}, \frac{2}{1}-2$	$2-\frac{2}{1}, \frac{2}{1}-2$	$2-\frac{2}{1}, \frac{2}{0}-2$	$2-\frac{2}{1}, \frac{2}{0}-2$
tibia	$2-\frac{2}{2}, \frac{2}{1}-2$	$1-\frac{1}{1}, \frac{2}{1}-1$	$1-\frac{1}{1}, \frac{2}{1}-1$	$1-\frac{1}{1}, \frac{2}{1}-1$

Coxa II without anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	120/66	108/60	114/54	135/54
tibia	120/60	102/60	108/54	132/48
tarsus	198/54	162/48	174/45	222/48

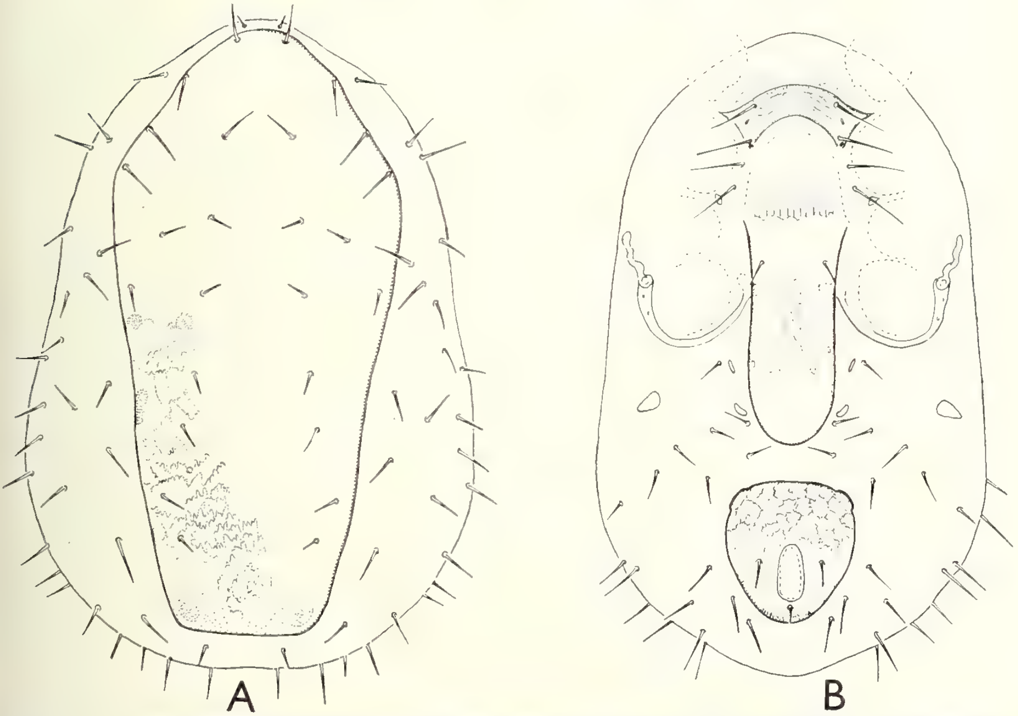

FIG. 98. *Dermanyssus chelidonis* Oudemans, female ; dorsum (A) and venter (B) of idiosoma.

Protonymph : Dorsal shield markedly attenuated posteriorly, extending to a point behind the level of setae *J2* (Text-fig. 97B) ; bearing nine pairs of setae, *j1* being on the shield. Opisthonotal region of dorsum with *J* series of setae complete.

HABITAT : In the nests of swallows (*Hirundo rustica* Linn.) in England and Italy.

Dermanyssus hirundinis (Hermann)

Acarus hirundinis Hermann, 1804, *Mémoire Aptérologique Strasbourg* : 83.
Dermanyssus hirundinis: Evans & Till, 1962, *Ann. Mag. nat. Hist.* (13) **5** : 285.

Female : Chelicera with second segment greatly elongated, digits minute, weakly dentate. Four pairs of gnathosomal setae with *c.s.* about 57 μ apart, *hyp.2* about 42 μ apart, *hyp.1* relatively stout. Deutosternum with ten denticles arranged in single file ; corniculi membranous with sclerotized bars. Tectum capituli elongate, triangular, with smooth margin. Pedipalp (2–4–6–12) with two-tined apotele.

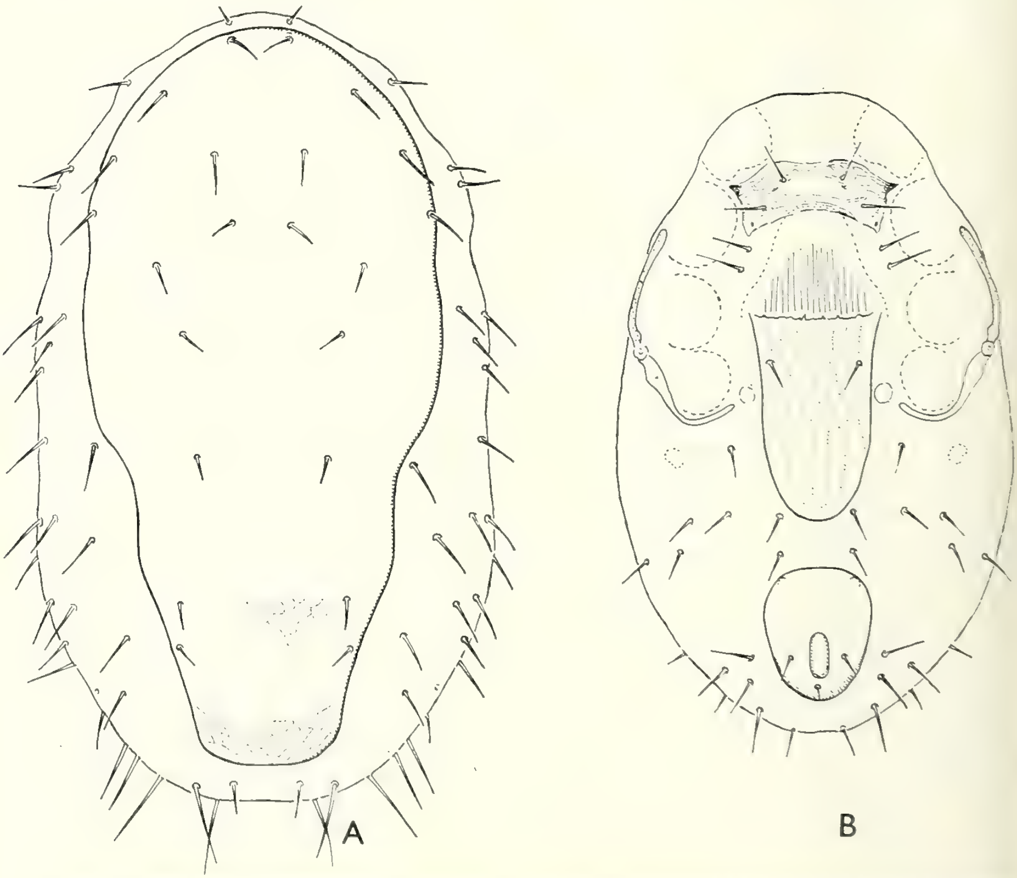

FIG. 99. *Dermanyssus hirundinis* (Hermann), female ; dorsum (A) and venter (B) of idiosoma.

Dorsal shield (680 μ × 294 μ) with 11 pairs of setae distributed as in Text-fig. 99A ; setae *j*1 and *J*5 off the shield, seta *J*2 missing. Surface of shield reticulated.

Tritosternum with base 60 μ, laciniae 84 μ, with hyaline denticulate margin. Sternal shield (42 μ × 130 μ) weakly reticulated, with two pairs of setae and two pairs of pores ; *st*3 and metasternals free on unsclerotized integument. Between *st*1, 63 μ ; between *st*1 and *st*3, 84 μ. Genital shield (180 μ × 110 μ) weakly reticulated, with genital setae only. Anal shield (130 μ × 105 μ ; maximum width 132 μ) with paranal setae 33 μ, postanal seta 18 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 99B. Peritreme extends to posterior third of coxa II ; anterior part of peritrematal shield not developed, posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs shows deviations affecting most segments, with some intraspecific variability ; protonymphal patterns retained on femur III and on tibiae II–IV :

	I	II	III	IV
femur	$2-\frac{5}{3}-2$	$2-\frac{5}{3}-1$	$1-\frac{3}{1}-0$	$0-\frac{3}{2}-1$
genu	$2-\frac{2}{2},\ \frac{2}{1}-2$	$1/2-\frac{1/2}{1},\ \frac{1/2}{1/0}-1$	$1-\frac{2}{1},\ \frac{2}{0}-1$	$1-\frac{2}{1},\ \frac{2}{0}-1$
tibia	$2-\frac{2}{2},\ \frac{2}{1}-2$	$1-\frac{1}{1},\ \frac{2}{1}-1$	$1-\frac{1}{1},\ \frac{2}{1}-1$	$1-\frac{1}{1},\ \frac{2}{1}-1$

Coxa II without anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	90/48	75/45	60/42	80/40
tibia	90/45	72/45	66/40	90/38
tarsus	165/40	126/40	126/40	162/36

Male : Chelicera with segment I, 50 μ ; II, 90 μ ; fixed digit reduced, spermadactyl long (110 μ), grooved, completely fused with movable digit. Four pairs of gnathosomal setae with *c.s.* about 50 μ apart, *hyp.*2 about 50 μ apart, *hyp.*1 normal. Other gnathosomal features as in female.

Dorsal shield (570 μ × 282 μ) bearing 18 or 19 pairs of setae. In the podonotal region setae *j*1, *s*1, *s*3, *r*3 and *s*5 are on the shield ; in the opisthonotal region *Z*1, *J*5 and sometimes *Z*4 are on the shield. Surface of shield reticulated.

Tritosternum with base 42 μ, laciniae 66 μ, with hyaline denticulate border. Holoventral shield (468 μ × 108 μ) reticulated, with five pairs of setae in the sternitogenital region, two pairs in the ventral region and the usual three anal setae. Between *st*1, 52 μ ; between *st*1 and *st*3, 108 μ. Paranal setae 27 μ, postanal seta 15 μ long. Peritreme extends to middle of coxa II ; peritrematal shield fused posteriorly with podal elements of coxa IV.

Chaetotaxy of legs as in female ; seta pv_2 on tarsi III and IV modified to form tooth-like structures. Coxa II without anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	75/42	60/45	60/42	78/45
tibia	75/40	51/42	60/42	78/42
tarsus	114/34	75/36	—	—

Protonymph : Gnathosomal structures, excluding pedipalps, essentially as in female, but not so well developed. Four pairs of gnathosomal setae with *c.s.* about 36 µ apart, *hyp.*2 about 32 µ apart. Pedipalps with normal chaetotaxy (1–4–5–12) for this instar.

Podonotal shield (312 µ × 120 µ ; maximum width 198 µ) with slender posterior prolongation of variable length (Text-fig. 97D), bearing eight pairs of setae, *j*1 being off the shield. Opisthonotal region of dorsum with four pairs of *J* setae, *J*2 being absent.

Tritosternum with base 36 µ, laciniae 70 µ. Sternal shield (180 µ × 102 µ) with three pairs of setae and two pairs of pores. Between *st*1, 48 µ ; between *st*1 and *st*3, 108 µ. Genital setae absent. Anal shield (84 µ × 57 µ ; maximum width 75 µ) ; paranal setae 24 µ, postanal seta 16 µ long ; Opisthogastric cuticle with six pairs of setae. Peritreme extends to middle of coxa III.

Chaetotaxy of legs normal for this instar. Coxa II without anterior spine. Length width (in µ) of leg segments :

	I	II	III	IV
genu	51/39	45/38	42/34	51/34
tibia	54/36	45/36	42/34	51/34
tarsus	98/32	93/30	90/30	98/28

Deutonymph : Gnathosoma essentially as in female. Four pairs of gnathosomal setae with *c.s.* about 45 µ apart, *hyp.*2 about 36 µ apart.

Dorsal shield (522 µ × 198 µ) with chaetotaxy as in female.

Tritosternum with base 50 µ, laciniae 70 µ. Sternito-genital shield (270 µ × 108 µ) with three pairs of sternal setae, one pair of metasternal and one pair of genital setae, the metasternals and genitals being relatively short and fine. Between *st*1, 60 µ ; between *st*1 and *st*3, 110 µ. Anal shield (105 µ × 80 µ ; maximum width 96 µ) with paranal seta 24 µ, postanal seta 12 µ long. Integument of opisthogaster with 10 pairs of setae. Peritreme extends to posterior margin of coxa II ; peritrematal shields apparently not developed.

Chaetotaxy of legs as in female. Coxa II without anterior spine. Length/width (in µ) of leg segments :

	I	II	III	IV
genu	69/45	60/42	51/40	63/36
tibia	72/42	57/40	54/36	72/36
tarsus	135/36	98/34	96/33	114/32

HABITAT : Recorded in Britain from *Hirundo rustica* Linn.

Dermanyssus alaudae (Schrank)

Acarus alaudae Schrank, 1781, *Enum. Ins. Austriae* : 515.
Dermanyssus alaudae: Evans & Till, 1962, *Ann. Mag. nat. Hist.* (13) **5** : 279.
Acarus truncatus von Olfers, 1816, *De Vegetativis etc. Commentarius* **1** (5) : 71.

Female : Chelicera with segment II greatly elongated, digits minute. Four pairs of gnathosomal setae with *c.s.* about 36 μ apart, *hyp*.2 about 36 μ apart ; *hyp*.1 relatively stout. Deutosternum with denticles arranged in a single longitudinal file. Corniculi membranous with sclerotized bars. Tectum capituli elongate, triangular, with smooth margin. Pedipalp (2–4–5–7/8) with two-tined apotele.

Dorsal shield (576 μ × 300 μ) with ten pairs of setae distributed as in Text-fig. 100A ; setae *j*1 and *J*5 lie off the shield ; setae *j*3, *j*4 and *J*2 are absent. Seta *s*4 considerably longer than the setae of the hexagon (*j*5, *z*5, *j*6). A well defined pore is located on each side of the shield slightly posterior to seta *s*4. Surface of shield without a well defined pattern.

Tritosternum with base 30 μ, laciniae 66 μ ; with hyaline denticulate margin. Sternal shield (approximately 24 μ × 120 μ) weakly sclerotized, usually with one pair of setae ; *st*2 and *st*3 free on unsclerotized integument, metasternals absent.

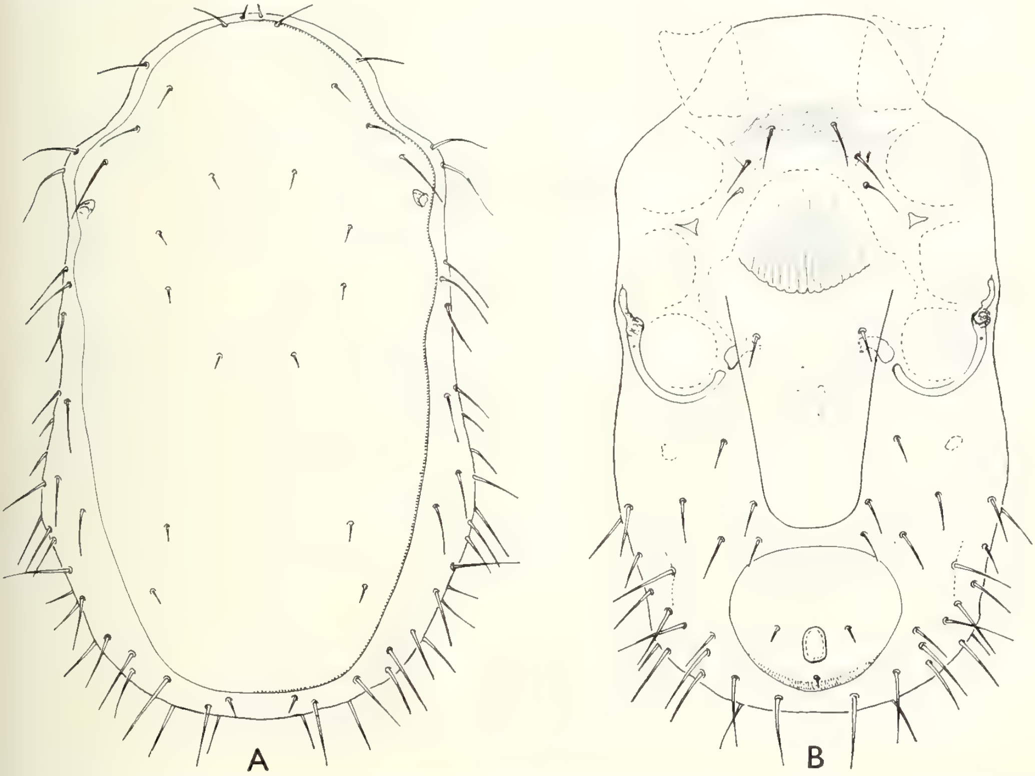

FIG. 100. *Dermanyssus alaudae* (Schrank), female ; dorsum (A) and venter (B) of idiosoma.

Between *st*1, 48 μ; between *st*1 and *st*3, 57 μ. Genital shield (162 μ × 120 μ) with no definite pattern and bearing genital setae only. Anal shield (108 μ × 120 μ; maximum width 135 μ) with paranal setae 20 μ, postanal seta 9 μ long. Chaetotaxy and sclerotization of opisthogaster as in Text-fig. 100B. Peritreme very short, extending to middle of coxa III; peritrematal shield not developed anteriorly, posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs shows deviations from the normal pattern on most segments, including trochanter I which lacks a dorsal seta ($1\text{—}\frac{0}{3}\text{—}1$). Protonymphal patterns are retained on femora I and III, genua II and III and tibiae II–IV:

	I	II	III	IV
femur	$2\text{—}\frac{4}{2}\text{—}2$	$1\text{—}\frac{4}{3}\text{—}1$	$1\text{—}\frac{3}{1}\text{—}0$	$1\text{—}\frac{3}{1}\text{—}0$
genu	$2\text{—}\frac{2}{1}, \frac{2}{1}\text{—}2$	$1\text{—}\frac{2}{0}, \frac{2}{0}\text{—}1$	$1\text{—}\frac{2}{0}, \frac{2}{0}\text{—}1$	$1\text{—}\frac{2}{1}, \frac{2}{0}\text{—}1$
tibia	$2\text{—}\frac{2}{1}, \frac{2}{1}\text{—}2$	$1\text{—}\frac{1}{1}, \frac{2}{1}\text{—}1$	$1\text{—}\frac{1}{1}, \frac{2}{1}\text{—}1$	$1\text{—}\frac{1}{1}, \frac{2}{1}\text{—}1$

Coxa II without anterior spine. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	57/50	60/48	50/48	60/45
tibia	54/48	54/48	50/45	60/45
tarsus	102/42	102/40	96/40	120/38

Protonymph: Gnathosoma, excluding pedipalps, as in female, but not so well developed. Four pairs of gnathosomal setae with *c.s.* about 27 μ apart, *hyp.*2 about 27 μ apart. Pedipalp (1–4–4/5–8) with minute, two-tined apotele.

Podonotal shield attenuated posteriorly to form a fairly acute point; with seven pairs of setae distributed as in Text-fig. 97C; *j*1 is off the shield and *j*3 and *j*4 are absent. Opisthonotal region with several small, ill-defined scutellae; setae *J*2 absent.

Tritosternum biramous; sternal shield sometimes with a weakly sclerotized posterior extension, with three pairs of setae and two pairs of pores. Between *st*1, 56 μ; between *st*1 and *st*3, 102 μ. Genital setae absent. Anal shield (63 μ × 72 μ; maximum width 80 μ), paranal setae 15 μ, postanal seta 10 μ long. Opisthogastric cuticle with six pairs of setae. Stigma at level of middle of coxa IV, peritreme extending to anterior margin of coxa IV.

Chaetotaxy of legs normal for this instar except for femora II and III which have seven and five setae respectively. Coxa II without anterior spine. Length/width (in μ) of leg segments:

	I	II	III	IV
genu	33/42	33/33	24/36	30/36
tibia	30/40	30/36	27/33	30/33
tarsus	72/30	63/30	63/27	72/27

HABITAT: Recorded from *Alauda arvensis* Linn. in Scotland and Europe (Austria).

Dermanyssus quintus Vitzthum

Dermanyssus quintus Vitzthum, 1921, *Arch. Naturgesch.* (A) **86** : 7.
Evans & Till, 1962, *Ann. Mag. nat. Hist.* (13) **5** : 286.

Female : Chelicera with segment II greatly elongated, digits minute, weakly dentate. Four pairs of gnathosomal setae with *c.s.* about 42 μ apart, *hyp.*2 about 36 μ apart ; *hyp.*1 relatively stout. Deutosternum with ten denticles arranged in a single longitudinal file. Corniculi membranous with sclerotized bars. Tectum capituli elongate, triangular, with smooth margin. Pedipalp (2–4–6–12) with two-tined apotele.

Dorsal shield (672 μ × 336 μ) with 11 pairs of setae distributed as in Text-fig. 101A ; setae *J*5 off the shield, *J*2 absent. Setae *j*2, *z*2 and *z*4 considerably longer than the remaining setae on the shield. Surface of shield weakly reticulate, with sculpturing anteriorly.

Tritosternum biramous, with hyaline denticulate margin. Sternal shield (approximately 40 μ × 140 μ) with a more strongly sclerotized central portion ; bearing two pairs of setae and one pair of pores ; *st*3 and metasternals free on unsclerotized integument. Between *st*1, 72 μ ; between *st*1 and *st*3, 90 μ. Genital shield (174 μ × 60 μ) with weakly defined linear markings and bearing genital setae only. Anal shield (112 μ × 138 μ ; maximum width 174 μ) with paranal setae about 27 μ long. Opisthogastric cuticle bears a prominent arc of stout setae (Text-fig. 101B). Peri-

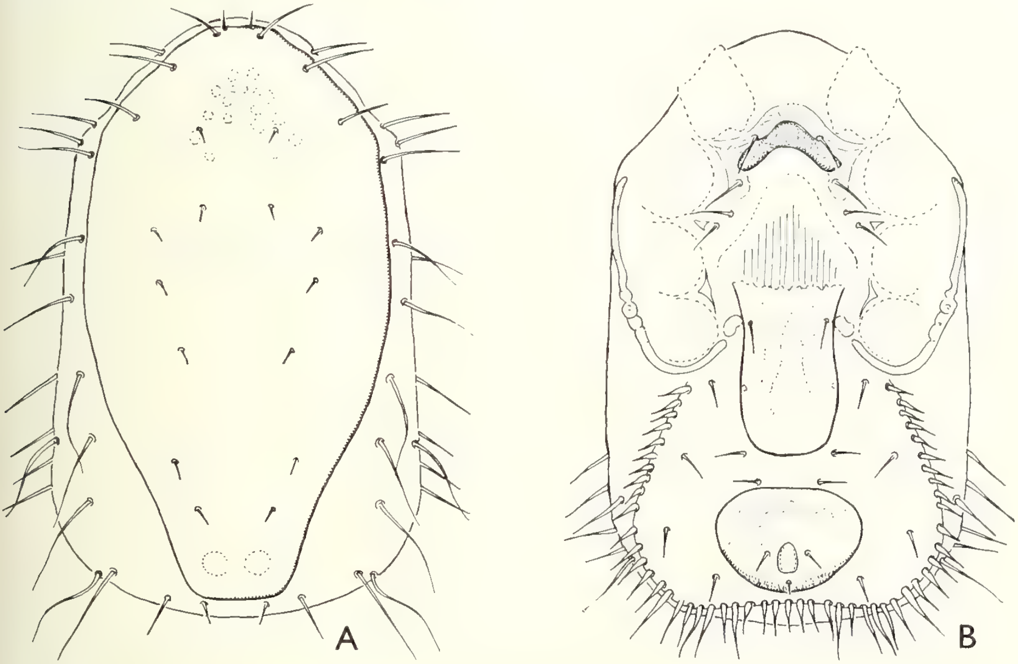

FIG. 101. *Dermanyssus quintus* Vitzthum, female ; dorsum (A) and venter (B) of idiosoma.

treme extends to middle of coxa II ; peritrematal shield not developed anteriorly, posterior part fused with podal elements of coxa IV.

Chaetotaxy of legs shows deviations from the normal on most segments, with retention of the protonymphal patterns on tibiae II–IV :

	I	II	III	IV
femur	$2-\frac{5}{3}-2$	$1-\frac{5}{3}-1$	$1-\frac{3}{1}-1$	$1-\frac{3}{1}-1$
genu	$2-\frac{3}{1}, \frac{2}{1}-1$	$2-\frac{2}{1}, \frac{2}{1}-1$	$1-\frac{2}{1}, \frac{2}{0}-1$	$1-\frac{2}{1}, \frac{2}{0}-1$
tibia	$2-\frac{2}{1}, \frac{2}{1}-1$	$1-\frac{1}{1}, \frac{2}{1}-1$	$1-\frac{1}{1}, \frac{2}{1}-1$	$1-\frac{1}{1}, \frac{2}{1}-1$

Coxa II without anterior spine. Length/width (in μ) of leg segments :

	I	II	III	IV
genu	78/60	78/66	69/60	75/57
tibia	78/57	75/63	66/57	72/54
tarsus	128/51	126/52	120/50	138/48

HABITAT : Recorded from *Dendrocopos major* (Linn.) in Britain, and from *Dendrocopos leucotos* (Bechstein) and *D. major* in Germany and the U.S.S.R.

SPECIES INCERTAE SEDIS

We have been unable to examine the type material of the following species of Dermanyssidae recorded from Britain and Eire. The original descriptions are inadequate for their certain identity.

Eulaelaps affinis Hull, 1925 (♂ and ♀), possibly a synonym of *Eulaelaps stabularis* (Koch).

Eulaelaps lapidarius Hull, 1925 (♀), possibly a synonym of *Pseudolaelaps doderoi* Berlese.

Hypoaspis fucorum Hull, 1925 (♂), referable to *Hypoaspis* (*Pneumolaelaps*).

Hypoaspis latifrons Hull, 1925 (♀), referable to *Hypoaspis* (*Gaeolaelaps*).

Hypoaspis nitidissimus Hull, 1918 (♀), possibly a synonym of *Haemogamasus pontiger* (Berlese).

Hypoaspis soricinus Hull, 1925 (♂).

Laelaps (*Hypoaspis*) *longipes* Halbert, 1915 (♂), possibly a synonym of *Haemogamasus horridus* Michael.

Laelaps (*Hypoaspis*) *ovatulus* Halbert, 1915 (♀), referable to *Pseudoparasitus*.

Laeliphis birksianus Hull, 1925 (♀), referable to *Hypoaspis* (*Gymnolaelaps*) .

Laeliphis fuscipes Hull, 1925 (♂ and ♀), referable to *Hypoaspis* (*Gymnolaelaps*).

SUMMARY OF NEW TAXA AND SYNONYMY

1. The following new taxa are proposed :

   subfamilies : Hirstionyssinae nov., Melittiphinae nov. and Pseudolaelapinae nov.

genus : *Domrownyssus* nov., type : *Pneumonyssus dentatus* Domrow, 1961 (Laelapinae)

species and subspecies : *Hirstionyssus oryctolagi* nov., *Hypoaspis breviseta* nov., *Hypoaspis colomboi* nov., *Hypoaspis giffordi* nov., *Hypoaspis hyatti* nov., *Hypoaspis neocuneifer* nov., *Hypoaspis nidicorva* nov., *Hypoaspis casalis myrmecophila* nov.

2. The following new synonymy is presented :

Allonyssus Buitendijk, 1945, a synonym of *Macronyssus* Kolenati
Austrogamasellus Domrow, 1957, a synonym of *Pseudoparasitus* Oudemans
Daviseilla Zumpt & Patterson, 1951, a synonym of *Stratiolaelaps* Berlese
Groschaftella Samsinak, 1957, a synonym of *Haemogamasus* Berlese
Sauronyssus Sambon, 1928, a synonym of *Ophionyssus* Mégnin
Cosmolaelaps gurabensis Fox, 1946, a synonym of *Hypoaspis miles* (Berlese)
Eulaelaps kolpakovae Bregetova, 1950, a synonym of *Eulaelaps novus* Vitzthum
Hypoaspis compressus Hull, 1925, a synonym of *Hypoaspis lubrica* Voigts & Oudemans
Hypoaspis nolli Karg, 1962, a synonym of *Hypoaspis praesternalis* Willmann
Hypoaspis soarianus Hull, 1925, a synonym of *Androlaelaps casalis casalis* (Berlese)
Ichoronyssus orcadensis Turk, 1946, a synonym of *Hirstionyssus latiscutatus* (de Meillon & Lavoipierre)
Laelaspis ovatus Willmann, 1951, a synonym of *Hypoaspis astronomica* (Koch)
Laelaps pachypus : Oudemans, 1927 (male), a synonym of *Hyperlaelaps microti* (Ewing)
Laelaps pachypus : Oudemans, 1927 (female) a synonym of *Hyperlaelaps amphibia* Zachvatkin
Laelaps (*Hyperlaelaps*) *arvalis* Zachvatkin, 1948, a synonym of *Hyperlaelaps microti* (Ewing)
Pseudoparasitus angulatus Berlese, 1917 a synonym of *Laelaps* (*Hypoaspis*) *oblonga* Halbert, 1915.
Liponyssus rhinolophi Oudemans, 1902, a synonym of *Macronyssus uncinatus* (Canestrini)
Ololaelaps halaskovae Bregetova & Koroleva, 1964, a synonym of *Ololaelaps veneta* (Berlese).

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ABREVIATIONS USED IN TEXT AND FIGURES

ad_{1-3}	antero-dorsal setae
al_{1-3}	antero-lateral setae
av_{1-3}	antero-ventral setae
c.s.	capitular setae
d_{1-3}	dorsal setae
d.l.f.	dorsal lyriform fissure
d.s.	dorsal seta
f.d.	fixed digit
gen.	genital setae
hyp. 1–3	hypostomal setae
*j*1–6	dorsal series of podonotal setae
*J*1–5	dorsal series of opisthonotal setae
*Jv*1–5	internal ventral setae
lat.l.f.	lateral lyriform fissure
m.d.	movable digit
*p*1–3	sternal pores
p.d.	pilus dentilis
pd_{1-3}	postero-dorsal setae
pl_{1-3}	postero-lateral setae
pv_{1-2}	postero-ventral setae
*px*1–3	posterior accessory setae
*r*2–6	marginal series of podonotal setae
*R*1–7	marginal series of opisthonotal setae

*s*1–6	lateral series of podonotal setae
*S*1–5	lateral series of opisthonotal setae
sp.	spermadactyl
*st*1–3	sternal setae
*st*4	metasternal setae
UR	submarginal series of opisthonotal setae
v_{1-2}	ventral setae
*z*1–6	median series of podonotal setae
*Z*1–5	median series of opisthonotal setae
*Zv*1–5	medio-lateral ventral setae

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A REVIEW OF THE GENUS *PHILETOR* (CHIROPTERA : VESPERTILIONIDAE)

J. E. HILL

BULLETIN OF
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BY

J. E. HILL
Department of Zoology, British Museum (Natural History)

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A REVIEW OF THE GENUS *PHILETOR* (CHIROPTERA : VESPERTILIONIDAE)

By J. E. HILL

SYNOPSIS

The genus *Philetor* is reviewed and its geographical distribution extended from New Guinea to Malaya by the inclusion of *Eptesicus verecundus* Chasen, 1940. Particular attention is given to features considered of value in determining the affinities of the genus within the Vespertilioninae and its relationships are examined in detail.

INTRODUCTION

The vespertilionid genus *Philetor* with type species *P. rohui* was described by Thomas (1902) from a series of ten specimens obtained in the Albert Edward Mountains, Papua, New Guinea. Since that time, additional specimens of *P. rohui* from New Guinea have been received by the British Museum (Natural History) and, with the original series, these form the basis of this brief review. At the same time, an examination has been made of the holotype of *Eptesicus verecundus*, described by Chasen in 1940 from Malaya and apparently so far known only from this and one other specimen. The holotype proves referable not to *Eptesicus* but to *Philetor*, Chasen having failed to note the salient features of the external genitalia and skull. The major features of *Philetor* as thus understood have been studied with a view to establishing the relationships of this small but interesting genus.

PHILETOR Thomas

Philetor Thomas, 1902 : 220. Type species *Philetor rohui* Thomas.

A study of the genera *Pipistrellus*, *Nyctalus*, *Eptesicus*, *Tylonycteris* and *Mimetillus* indicates that apart from its curiously specialized external genitalia (which are approached in some respects by *Tylonycteris* and *Mimetillus*) there are no other exclusive diagnostic characters which serve to isolate *Philetor* as sharply as was thought by Thomas or by Miller (1907 : 213). However, it may be distinguished readily by a number of features in combination. The wings are narrow, with the fifth digit much reduced, its total length equal approximately to the combined length of the metacarpal and one-half of the length of the first phalange of the fourth digit. The braincase is high and rounded, the supraorbital region inflated with prominent supraorbital tubercles. The inner upper incisor (i^2) is bifid and is long and narrow in contrast to the outer upper incisor (i^3), which is small and conical. There is a prominent secondary posterior upper canine cusp and the small anterior upper premolar (pm^2) is lacking. The sole upper premolar (pm^4) and the second lower premolar (pm_4) are very much shortened so that their length at the cingulum is equal to approximately one-half of their width and at the alveolus is equal approximately to one-third of their width. The third upper molar (m^3) is not reduced and has three well-defined commissures.

Philetor rohui Thomas

The head is short and broad, with a wide, flattened muzzle, the narial openings sublateral, widely separated and not projecting. The anterior part of the muzzle is sparsely clothed with hair, with a distinct fringe of hairs on the upper lip. The ears are short, triangular in outline and rounded at the tip. There is a small lobe at the base of the anterior margin of the ear, above which the anterior margin is strongly convex near its base but is otherwise straight or nearly so, the posterior margin of the ear being slightly convex in its upper and lower parts, these separated by a shallow concavity. There is a small antitragal lobe, the posterior margin of the ear terminating behind and slightly below the angle of the mouth. There are a few sparse hairs on the anterior part of both the internal and external faces of the ear. The tragus is short, thick and fleshy, its anterior margin straight for its basal half but otherwise slightly convex, the upper part of the tragus slightly prolonged anteriorly. The upper margin of the tragus is slightly convex and its posterior margin slightly so or straight, with a small triangular lobe near the base. This lobe is absent in the holotype of *verecundus* but apparently has been destroyed during the extraction of the skull from the specimen in alcohol. The wing is narrow, with the fifth digit much reduced, its total length exceeding the length of the metacarpal of the fourth digit only by one-half of the length of the first phalange of the fourth digit. The metacarpal of the fifth digit is by far the shortest of the metacarpals and the combined lengths of the two terminal phalanges of the fifth digit are equal only to the length of the first phalange of the third digit. The thumb is short and stout. There is a distinct post-calcarial lobe supported by a robust calcar which extends along approximately one-half of the length of the posterior margin of the interfemoral membrane.

The genus is remarkable in the extraordinary complexity of the structure of the external genitalia. The penis (Text-fig. 1*a*–*b*) is long, with a stout shaft and large, prominent glans. It is densely pilose only at its base. Distally, the dorsal surface of the shaft (Text-fig. 1*a*) bears a cushion-like pad, on occasion divided to some extent by a longitudinal median depression. For much of its area this pad is moderately clothed with short, stiff bristles. The ventral surface of the shaft (Text-fig. 1*b*) is prolonged distally by a projecting preputial flap or fold, the slender stem of the glans penis emerging between its lateral lips which each bear a tuft of moderate, rather stiff hairs. According to Thomas (1902 : 221) the penis of *Philetor* lacks a prepuce : however, it seems evident that the flap or fold projecting from the lower part of the penial shaft is the lower or ventral lip of the prepuce, its upper or dorsal lip forming the anterior margin of the curious cushion-like pad which embellishes the distal part of the dorsal surface of the shaft. The glans penis is a swollen, approximately triangular structure pierced on its dorsal surface near the tip by the urethral opening. It is supported by a slender, upwardly curved stem which emerges from the tip of the shaft a little below its centre. Ventrally, the stem extends beneath the swollen glans penis almost to the tip and it is bordered by lateral fissures in the body of the glans : the underside of the stem has a median longitudinal groove extending almost to the point of emergence from the prepuce (Text-fig. 1*b*). The os penis or baculum (Text-fig. 1*c*–*e*) is strongly curved dorso-ventrally (Text-fig. 1*d*) and has a wide, deep flanged base, slender shaft and an expanded tip. Viewed dorsally (Text-fig. 1*c*) the base of the os penis forms a

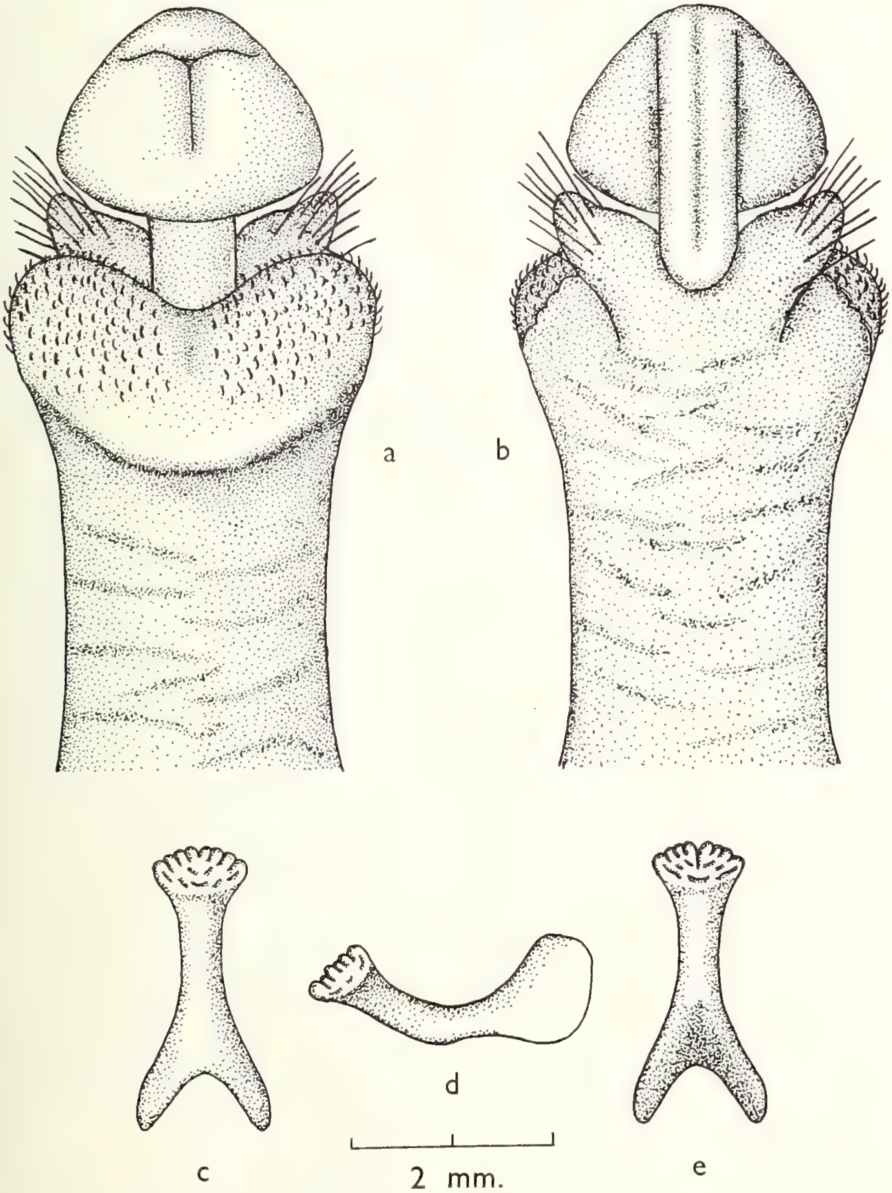

Fig. 1. *Philetor rohui rohui*. *a*, dorsal aspect of penis ; *b*, ventral aspect of penis ; *c*, dorsal aspect of os penis ; *d*, lateral aspect of os penis ; *e*, ventral aspect of os penis.

solid, bifid structure : ventrally (Text-fig. 1*e*) the base is hollowed, the medial groove thus formed extending to the base of the stem. As suggested by Thomas, the paired basal flanges evidently support the cushion-like pad on the dorsal surface of the penial shaft and the enlarged tip of the os penis supports the glans.

The external genitalia of the female (Text-fig. 2*a*–*b*) are similarly complex. The vulval opening is separated from the anus by paired, swollen perineal cushions or pads (Text-fig. 2*a*) which are divided by a median longitudinal groove and which have their surfaces sparsely covered with short hairs. Anterior to the vulval opening and normally partially concealing it there is a wide, subtriangular pad, partially divided longitudinally by a shallow median trough, its base anteriorly situated and with its apical part directed posteriorly and immediately above the vulval opening. This fleshy pad clearly corresponds to the prepuce of the male and a well-developed glans clitoris emerges from the fleshy fold forming its apical part (Text-fig. 2*a*). It is separated from the perineal pads by deep lateral fissures. There is a slightly swollen area forming a low cushion immediately posterior to the anus. The vulval opening is transverse, but also extends anteriorly as a narrow longitudinal slit (Text-fig. 2*b*) between fleshy lips, each with a small projecting spur posteriorly where they form the anterior rim of the transverse part of the vulval opening. No doubt this longitudinal slit led Thomas (1902 : 221) to his statement that the vulva was longitudinal instead of transverse : in fact the actual opening is transverse but is prolonged longitudinally. Posteriorly, the rim of the vulval opening is formed by the anterior walls of the perineal pads, which extend inwards in shelf-like fashion to form its posterior margin. Normally, the apical part of the subtriangular anterior pad fits into the shallowly V-shaped margin formed by the anterior part of the two perineal pads, thus concealing the vulval opening. The glans clitoris is normally concealed within the apical folds of this pad, its tip only being exposed. Thomas (1902 : 221) suggested that it appears probable that the slender projecting tip of the glans penis alone enters the vulva and the arrangement of cushion-like pads on the dorsal surface of the penis and on the perineum of the female supports this conclusion. The bristly pad on the dorsal surface of the penial shaft evidently engages with the perineal pads of the female during copulation while the tip of the glans clitoris engages in the groove beneath the stem supporting the glans penis.

All of the available specimens of *P. rohui* are preserved in alcohol. From these it appears that the dorsal surface of the body is uniformly dark brown, as is the head and nape : the ventral surface is similar in colour to the back but is slightly paler. As suggested by Thomas (1902 : 221) from the original series, which was even then in a bad state of preservation, the fur is short and close. It does not extend appreciably on to the flight membranes except for a sprinkling of fine hairs on the ventral surface of the wing from the body to a line joining the elbow and knee and for a few sparse hairs at the root of the tail.

The skull is short and wide, with short, wide, rounded braincase, its frontal part elevated. There is a slight occipital helmet with sharp lambdoidal ridges in older specimens. The sagittal crest is weak, dividing anteriorly into weak supraorbital

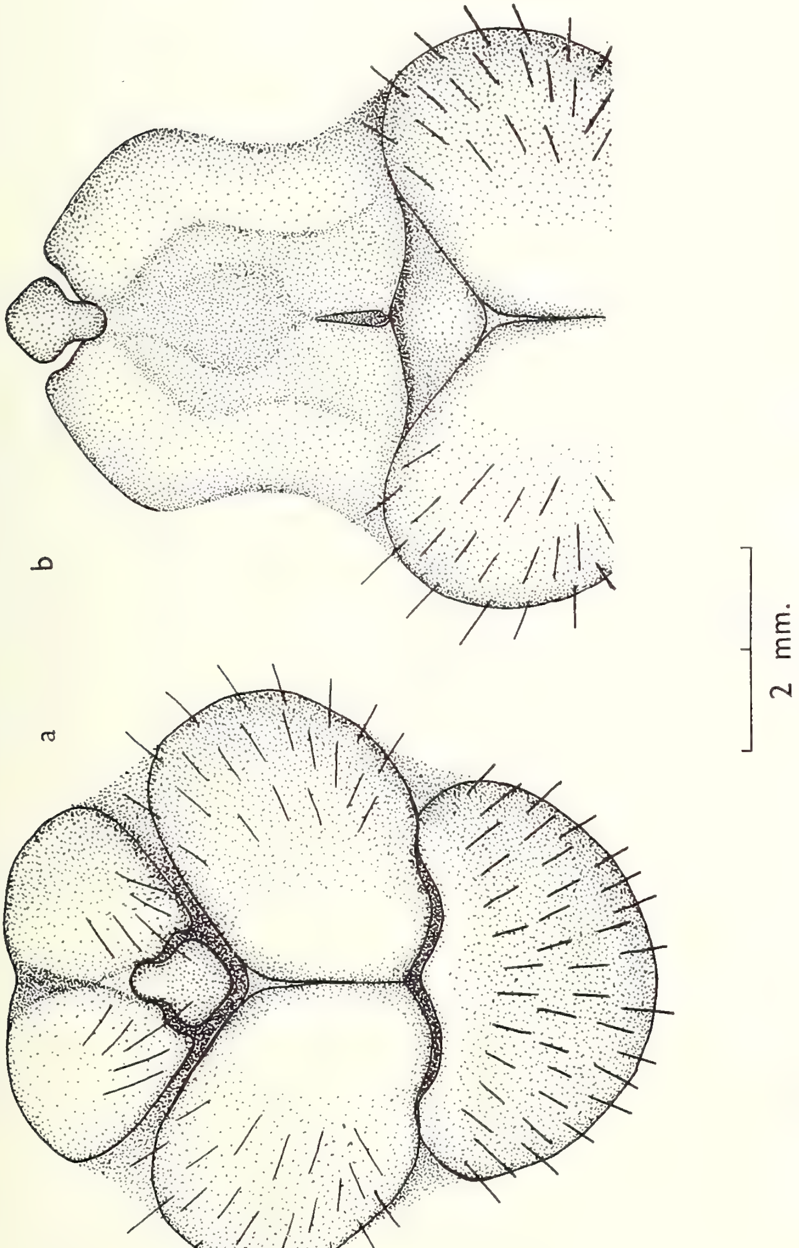

FIG. 2. *Philetor rohui rohui.* *a*, female external genitalia ; *b*, vulval opening exposed.

ridges which terminate in prominent supraorbital tubercles. The interorbital region is broad and the rostrum wide and rather high, the anteorbital foramen enclosed by a comparatively wide bar of bone. The zygomata are slender, in older specimens with a small inferior projection anteriorly, external to m^3. They are slightly widened posteriorly. The narial emargination is deep, extending posteriorly to a line joining the supraorbital tubercles and almost halfway to the interorbital constriction. The anterior palatal emargination is deep and is wide posteriorly, slightly chordate in outline, in older specimens with a median anterior palatal spine. The palate is short, wide and domed, with a large, blunt, ligulate post-palatal spine. The meso-pterygoid fossa is wide and there are moderate basial pits : the bullae are high and are slightly inflated.

The inner upper incisor (i^2) is elongate, narrow, and bicuspid, the posterior or outer cusp a little smaller and lower than the anterior or inner cusp. The outer upper incisor (i^3) is small and conical, its height only slightly exceeding the cingulum height of i^2, with a well-developed cingulum in contact or nearly so with the inner tooth. It is separated from the canine by a moderate diastema. The upper canine has a prominent posterior secondary cusp extending for one-third to one-half of the height of the tooth. The upper premolar (pm^4) is short, its length at the cingulum equal to approximately one-half of its width and it is tightly compressed between the canine and the first upper molar (m^1). The upper molars exhibit no especial peculiarities : m^3 is not reduced and has a prominent metacone and three well-defined commissures. The lower incisors are tricuspid and are not imbricated. They are situated in the line of the toothrow and are not turned at all transversely to it. The outer lower incisor (i_3) is very slightly wider than i_1 or i_2. The lower canine has small anterior and posterior cingulum cusps. The anterior lower premolar (pm_2) is equal in height to the second lower premolar (pm_4) and is comparatively unreduced, its length at the cingulum equal approximately to its width. The second lower premolar (pm_4) is much reduced, its length at the cingulum rather less than one-half of its width and with its posterior face hollowed where it engages with the anterior face of pm^4. Its crown area is equal to or barely exceeds the crown area of pm_2. The lower molars have no unusual features.

Philetor rohui rohui Thomas

Philetor rohui Thomas, 1902 : 220. Albert Edward Mountains, Papua, New Guinea, 6,000 ft.

Narial emargination not abruptly widened just above the roots of i^{2-2}. Minimum, maximum and (in parentheses) mean measurements (in millimetres) of fourteen specimens, except where stated : length of forearm (twenty specimens) 31·3–35·5 (33·4) ; greatest length of skull 13·4–14·8 (14·3) ; condylobasal length (thirteen specimens) 12·9–14·0 (13·6) ; least width of interorbital constriction 4·3–4·8 (4·6) ; zygomatic width (four specimens) 10·3–10·7 (10·5) ; width of braincase 7·3–8·2 (7·8) ; c-m^3 (front of canine to crown of m^3) 4·4–4·9 (4·7).

This subspecies is known so far only from New Guinea. It is recorded from specimens in the Archbold Collections of the American Museum of Natural History from

Oomsis, Morobe District and Kassam, Highlands District, in the Territory of New Guinea by Brass (1964 : 180, 204) who also (1956 : 136) records it from Biniguni Camp, Gwariu River, Papua, again from the results of the Archbold Expeditions. Tate (1942 : 265) records a specimen in the Archbold Collections from the Idenburg River, West Irian. Laurie (1952 : 313) recorded a series of specimens from Enaena, on the north-eastern slopes of Mount Simpson, eastern Papua, in the collection of the British Museum (Natural History). This collection also contains specimens from Dinawa, Owen Stanley Range, Papua and from Madeu, inland from Port Moresby, Papua. These are the specimens mentioned by Tate (1942 : 265).

Philetor rohui verecundus (Chasen)

Eptesicus verecundus Chasen, 1940 : 53. Mount Kladang, Perak, Federation of Malaya, 2,646 ft.

Narial emargination abruptly widened just above the roots of i^{2-2}. Chasen described *Eptesicus verecundus* from two specimens originally in the collection of the Raffles (now National) Museum, Singapore. That designated as the holotype is preserved in alcohol, with the skull extracted and was collected in November, 1916 by Dr. R. Hanitsch. Originally Raffles Museum No. 199, it was transferred to the British Museum (Natural History) in 1947 and is now B.M. 47.1437. The second example, also in alcohol with the skull extracted, came from an unspecified locality in Perak and remains in the National Museum, Singapore (Gibson-Hill, 1949 : 171). So far as I am aware, no further specimens have been obtained.

The original description compared *Eptesicus verecundus* with *E. pachyotis* (Dobson) and *E. demissus* Thomas, Chasen noting that it was smaller than either of these species. He remarked also that compared with *pachyotis* the body of *verecundus* is larger in relation to the wings, " as in *demissus* ". He had available for comparison specimens of *pachyotis* from the Khasia Hills, Assam, " very kindly sent to Singapore from the Indian Museum, Calcutta as the types of *pachyotis* some years ago . . . " and gives measurements of the length of forearm and lower leg with foot in these specimens. He states that the skulls had not been extracted, and his brief description of *verecundus* omits any mention of the structure of the external genitalia or of cranial features beyond noting that the inner incisor is much the larger and is tricuspid and that the upper canines have a small posterior secondary cusp. The description is otherwise concerned with external features such as the point of insertion of the wing membrane on the leg, and with the ears and tragus : he draws attention to the presence of a distinct post-calcarial lobe. Tate (1942 : 279) says " *Verecundus* obviously has peculiarities not seen elsewhere in *Eptesicus* " apparently solely on the basis of the published description.

An examination of the holotype of *Eptesicus verecundus* shows that in fact it is not an *Eptesicus* but is referable to *Philetor*, agreeing in almost every respect with *P. rohui* and differing only in a few minor and relatively insignificant points. The wing is reduced to almost exactly the same extent, with the fifth digit extending as far as a point slightly more than half-way along the first phalange of the fourth digit. The external genitalia of the female holotype are exactly as described for *P. rohui*. Cranially, there is a high degree of agreement but the braincase is a little more inflated than in *P. rohui* and the narial emargination is more abruptly widened just above the roots of i^{2-2}, with a broadly V-shaped apex. Although the supraorbital region has been damaged on both sides of the skull, the left side retains a prominent supraorbital tubercle: the corresponding tubercle on the right side of the skull has been lost. The inner upper incisor (i^2) is elongate and narrow, bicuspid, with a faint trace of a third posterior cusp which doubtless led Chasen to describe it as tricuspid. Measurements (in millimetres) of the holotype of *verecundus*: length of forearm 34·0; greatest length of skull —; condylobasal length 14·5; least width of interorbital constriction 4·7; zygomatic width —; width of braincase 7·9; c-m^3 (front of canine to crown of m^3) 4·7. The very close measure of agreement in structure and size between *verecundus* and *rohui* indicates that specific separation is unwarranted and for the present I consider them to be but subspecifically related.

The allocation of *verecundus* to *Philetor* clearly raises some question as to the status of *Eptesicus pachyotis* and *E. demissus*. The precise status of *E. pachyotis* seems uncertain (Tate, 1942 : 277) and unfortunately the collections of the British Museum (Natural History) contain no specimens referable to it. The descriptions by Dobson (1871 : 211, 1876 : 104, figs., 1878 : 206) are insufficient to enable any firm conclusions to be drawn, and the question must remain in abeyance until the holotype (Dobson, 1878 : 206) can be re-examined. It is presumably in the Indian Museum, Calcutta, whence Dobson described it. The collection of the British Museum (Natural History), however, does include the holotype of *E. demissus*. Externally, there is some similarity between this species and *verecundus* but *demissus* is considerably larger and the wings are not reduced, the fifth digit not conspicuously shortened but with its metacarpal nearly as long as the metacarpal of the fourth digit and with its tip reaching almost to the end of the first phalange of the fourth digit. The external genitalia of the female holotype lack the specialisations of *verecundus*. Cranially, the two are markedly dissimilar. The skull of the holotype of *demissus* is damaged but sufficient remains to demonstrate the presence of an occipital "helmet" and of a prominent sagittal crest. As Tate (1942 : 277) pointed out, the roof of the narial canal and of the anterior part of the mesopterygoid fossa is raised: in *verecundus* these lie deep in the skull. The inner upper incisor (i^2) of *demissus* is massive and wide, quite unlike the elongate, narrow i^2 of *verecundus* The outer upper incisor (i^3) is wide, its width exceeding its length, and has a large central cusp flanked by small lateral cusps. There is a low secondary posterior canine cusp but pm^4 is not shortened: i_{1-3} are considerably imbricated and pm_4 is not reduced, its length at the cingulum nearly equal to its width and its crown area exceeding that of pm_2. There seems no doubt that *demissus* has no close relationship to *verecundus* and thus to *Philetor* but instead apparently constitutes a distinct group within *Eptesicus*.

RELATIONSHIPS

Thomas (1902 : 220) considered *Philetor* allied to *Vespertilio* (= presumably to *Eptesicus* as understood by Miller (1907 : 207)), *Tylonycteris* and *Hesperoptenus*, also drawing attention to its resemblances to *Pterygistes* (= *Nyctalus*). Miller (1907 : 214) remarked that *Philetor* appeared related to *Tylonycteris* although lacking the flattening of the skull found in that genus. Subsequently, Tate (1942 : 266) thought that *Philetor* and *Tylonycteris* might be independently derived from near the *joffrei* group of *Pipistrellus,* and noted (pp. 252, 253, 265) the resemblances between the members of this group and *Philetor.* Evidently the relationships of *Philetor* are likely to be found within this complex of genera and their associated species : the absence of the small pm^2 in *Philetor* no doubt has influenced earlier authors in suggesting relationship to those genera in which this evanescent tooth is absent rather than to those in which it is present.

There appears to be no close relationship to *Hesperoptenus,* which has wings of normal proportions with the fifth digit unreduced in length. Although some modification of the penis has occurred in this genus, it is of a different nature to the specialisation of the penis in *Philetor,* as Thomas (1902 : 221) pointed out. In *Hesperoptenus* the prepuce is much developed and although the os penis is similarly divided at the base to that of *Philetor,* it is a much longer structure, straight and not upwardly curved and not expanded at its tip. Cranially, the braincase of *Hesperoptenus* is not elevated anteriorly and there are no supraorbital tubercles. The inner upper incisor (i^2) is a massive, unicuspid tooth, not elongate and narrow as in *Philetor* and i^3 in some species is displaced inwards to such an extent that it is situated behind the inner tooth. There is no secondary posterior canine cusp and $pm\frac{4}{4}$ are not shortened antero-posteriorly as in *Philetor,* with pm_2 much reduced.

Externally, there is a close resemblance between *Philetor* and *Eptesicus* but in that genus the wing is not reduced as it is in *Philetor.* The frontal part of the braincase is not elevated and there is little or no inflation of the supraorbital region. Prominent supraorbital tubercles are not developed in *Eptesicus.* Although bicuspid, i^2 is not elongate and narrow as in *Philetor* and i^3 is not especially reduced although smaller than the inner tooth. There is no secondary posterior canine cusp and $pm\frac{4}{4}$ are not shortened. The lower incisors are usually imbricated and pm_2 is reduced as in *Hesperoptenus.*

There is stronger evidence for a degree of relationship with *Tylonycteris.* As Tate (1942 : 266) has remarked, if the flattening of the skull in this genus be disregarded, then cranially and dentally it has a very close resemblance to *Philetor.* Externally, it differs from *Philetor* in the presence of pads on the thumbs and feet and the wing is not reduced but the penis has some similarity to that of *Philetor* and consists of a strong shaft with a large, expanded terminal pad like that of *Philetor,* similarly embellished with short, bristly hairs. On the dorsal surface of the shaft the pad is divided by a median longitudinal fissure to form swollen lateral cushions but ventrally it is less swollen although extending completely across the width of the shaft. There is no preputial fold such as is found in *Philetor* and the small glans penis emerges directly from a terminal perforation. The female external genitalia display none of the peculiarities of *Philetor.* There are no perineal pads although the vulval area is slightly swollen, and the vulval opening is wholly transverse without any median longitudinal extension. Cranially, there is some expansion of the supraorbital region in *Tylonycteris,* coupled with a varying degree of development of supraorbital tubercles, minimal in *T. pachypus* and its allies, maximal in *T. robustula* and *T. malayana*. There is on occasion a small, rather poorly-defined inferior zygomatic projection external to m^3 and the post-palatal spine is ligulate as in *Philetor*. The inner upper incisor (i^2) is elongate and narrow as in *Philetor*. It is similarly bicuspid, the posterior cusp as high or almost as high as the anterior cusp. The outer upper incisor (i^3) differs from that of *Philetor* and has a large central cusp equal in height or nearly equal in height to the posterior cusp of i^2, flanked by two smaller lateral cusps. It is slightly hollowed posteriorly. In *Philetor* this tooth is peg-like and conical: a faint trace of lateral cusps can be found only in the holotype of *verecundus*. The upper canine of *Tylonycteris* has a strong secondary posterior cusp and pm^4 is slightly shortened much as in *Philetor*, its length at the cingulum equal approximately to one-half of its width. The lower incisors (i_{1-3}) are slightly imbricated and pm_2 is but slightly reduced and is almost equal in height to pm_4, which is shortened in the same way as it is in *Philetor*, its length at the cingulum equal to one-half or to a little less than one-half of its width and its crown area equal to or only slightly exceeding the crown area of pm_2.

Great reduction of the wing is found in the Ethiopian genus *Mimetillus* which resembles *Tylonycteris* in the presence of pads on the thumbs and feet and to which it has been considered (Allen, 1939 : 194) to be related. In *Mimetillus* the reduction of the wing is not confined only to shortening of the fifth digit as in *Philetor* but extends also to shortening of the third digit, a feature unremarked in any other bat. The penis of *Mimetillus* does not resemble that of *Tylonycteris* or of *Philetor* at all closely. It is long and is wide at the base, tapering to a narrow tip. The shaft has no terminal pad such as occurs in these genera, its conical distal half instead being only slightly expanded and covered with short, bristly hairs. There is a small terminal opening through which protrudes the glans penis. The female external genitalia display some similarity to those of *Philetor*. The vulval opening is separated from the anus by paired, small poorly-developed perineal pads and there is a prominent posteriorly directed fold anterior to the opening which covers it and is slightly triangular in outline, a fissure at the apex indicating the glans clitoris. The vulval opening is wholly transverse and has no median longitudinal extension as in *Philetor*. The skull of *Mimetillus* is flattened as is the skull of *Tylonycteris* and the supraorbital region is much widened by the great degree of inflation of the maxillaries above the anteorbital foramina: as Tate (1942 : 266, footnote) has pointed out, these swellings are not strictly homologous with the supraorbital tubercles of *Tylonycteris* (and *Philetor*) but instead are "swellings of the area anterior to that part of the orbit which encloses the anteorbital foramen, but posterior to the foramen". It is the upper part of the bar enclosing the foramen and the part of the maxilla immediately adjacent which is swollen. The zygomata are massive, in contrast to the slender zygomata of *Philetor* and *Tylonycteris*. The inner upper incisor (i^2) is less markedly elongated than in *Philetor* or *Tylonycteris* but is bicuspid as it is in those genera. The outer upper incisor (i^3) is almost exactly like the corresponding tooth in *Tylonycteris*. There is no secondary posterior canine cusp but pm^4 is reduced to about the same extent as it is in *Philetor* and *Tylonycteris*.

its length at the cingulum equal approximately to one-half of its width. The lower incisors are imbricated. There is a marked difference between *Mimetillus*, *Philetor* and *Tylonycteris* in the proportions of the lower premolars : in *Mimetillus* pm_2 is very much reduced, almost peg-like, its height not exceeding one-half of the height of pm_4 and its crown area approximately one-quarter of the crown area of that tooth, which is not especially shortened, its length at the cingulum rather more than one-half of its width. Despite some similarities to *Philetor* and to *Tylonycteris*, a number of features of *Mimetillus* indicate that it has no very close relation to either of these genera, and Tate (1942 : 266) has remarked that certain of its characteristics suggest that it may be of independent origin.

In the original description Thomas (1902 : 220) noted that *Philetor* resembled *Nyctalus* in its general appearance and in its much shortened fifth finger. It must be remembered, however, that at the time that Thomas wrote, the genus *Nyctalus* was held to include the species *joffrei*, *stenopterus* and *brachypterus* subsequently removed by Tate (1942 : 252) to form the *joffrei* group of *Pipistrellus*. There is no immediate connection between *Philetor* and *Nyctalus* as thus restricted. As understood by Tate, *Nyctalus* has a high, convex frontal region and high rostrum as in *Philetor* but the rostrum is less widened and supraorbital tubercles are lacking. There is no inferior zygomatic projection and the post-palatal process is spine-like. The inner upper incisor (i^2) is massive, its length equal approximately to its width, and its posterior cusp is obsolete The outer upper incisor (i^3) is wider than long and is deeply concave posteriorly, with a small secondary posterior cusp. There is no secondary posterior canine cusp and pm^2 is present, $pm\frac{4}{4}$ being only slightly shortened. The lower incisors are imbricated and pm_2 is much reduced, its crown area one-half or less than one-half of the crown area of pm_4.

The nearest relatives of *Philetor* appear to be found in the *joffrei* group of *Pipistrellus* (more correctly the *brachypterus* group), created by Tate (1942 : 251) to include the three species *joffrei*, *stenopterus* and *brachypterus*, all formerly included within *Nyctalus*, together with a fourth, *anthonyi*, which he described in that paper (p. 252). Ellerman and Morrison-Scott (1951 : 159), however, retain *joffrei* in *Nyctalus* but (p. 173) leave *anthonyi* in *Pipistrellus*. Of these four species, only *joffrei* and *stenopterus* are available to me. The members of the *joffrei* group have the wing reduced to a greater or lesser extent by shortening of the fifth digit. The rostrum in these species is short and wide, with incipient or moderately developed supraorbital tubercles and on occasion there is an inferior descending zygomatic process external to m^3. The outer upper incisor (i^3) is small and a secondary posterior canine cusp is present : pm^2 is minute, pm_2 unreduced and $pm\frac{4}{4}$ shortened anteroposteriorly. There is considerable justification for the removal of this group of species from *Nyctalus* since apart from the reduced wing and the presence of a minute pm^2 these features are anomalous in that genus as otherwise understood. In fact, the *joffrei* group of species displays a number of the features characteristic of *Philetor*. Tate (1942 : 252) notes that the group approaches the Oriental members of the *savii* group of *Pipistrellus* in which pm^2 is minute and the palate shortened but which have not developed supraorbital tubercles.

So far as I am able to determine from the material available to me and from the literature *Pipistrellus joffrei* and *P. anthonyi* appear to be the most greatly modified members of the group. The collection of the British Museum (Natural History) contains the male holotype of *P. joffrei* B.M. 88.12.1.37, from the Kachin Hills, Burma, and also three female examples, B.M. 16.3.26.2, 83, 84, from 50 miles west of Kindat, Chindwin, Burma The ear and tragus closely resemble those of *Philetor* and the fifth digit is correspondingly reduced, its metacarpal conspicuously shorter than the metacarpal of the fourth digit and its tip reaching a point approxiately half-way along the first phalange of the fourth digit The external genitalia (Text-fig. 3), however, differ from those of *Philetor* although in some respects those of the male conform closely to the same pattern. The penis (Text-fig. 3*a–b*) is shorter than that of *Philetor* and the dorsal surface of the shaft bears a similar but less developed bristly pad in its distal part. This pad is less swollen and less extensive than in *Philetor*. The preputial fold is well developed and originates a little below this rudimentary pad, from which it is clearly demarcated. It is sparsely scattered with short hairs and has a shallow median longitudinal fissure in its dorsal surface and a relatively large terminal opening. Through this protrudes the small glans penis, which is perforated near its tip by the urethral opening. So far as can be discovered, an os penis, if present, must be very small and rudimentary. The female external genitalia (Text-fig. 3*c*) are not specialized as in *Philetor*. There are no perineal pads as in that genus, the vulval area being only slightly swollen, and the vulval opening is wholly transverse with no median longitudinal extension. The lips of the vulva protrude slightly and the glans clitoris is represented by a small protuberance immediately anterior to the vulval opening.

The skull of *Pipistrellus joffrei* is very like that of *Philetor* in its general appearance, but the braincase is more elevated posteriorly and a little less so anteriorly. The rostrum is rather less elevated and usually the supraorbital tubercles are not as much developed. There is a small inferior descending zygomatic process external to m^3. The palate is relatively a little narrower than in *Philetor* and has a similarly ligulate post-palatal spine. The inner upper incisor (i^2) is elongate as in *Philetor* but is relatively very slightly wider. It is bicuspid as in that genus, the posterior cusp nearly as high as the anterior cusp. The outer upper incisor (i^3) is wide, less reduced than in *Philetor*, and is much hollowed posteriorly. It has a large central cusp flanked by smaller lateral cusps, the postero-external cusp obsolescent, the antero-internal cusp with a small subsidiary cusp below it. There is a well-developed secondary posterior canine cusp. The anterior upper premolar (pm^2) is very small and is situated in the angle or recess formed by the base of the posterior canine cusp, the postero-internal part of the canine cingulum and the anterior face of pm^4, which is slightly shortened antero-posteriorly, its length at the cingulum a little more than one-half of its width. The third upper molar is unreduced, with a well-developed metacone and three commissures. The lower incisors (i_{1-3}) are not imbricated and pm_2 is not reduced, its height nearly equal to that of pm_4 and its crown area equal approximately to the crown area of that tooth, which is slightly shortened antero-posteriorly, its length at the cingulum slightly exceeding one-half

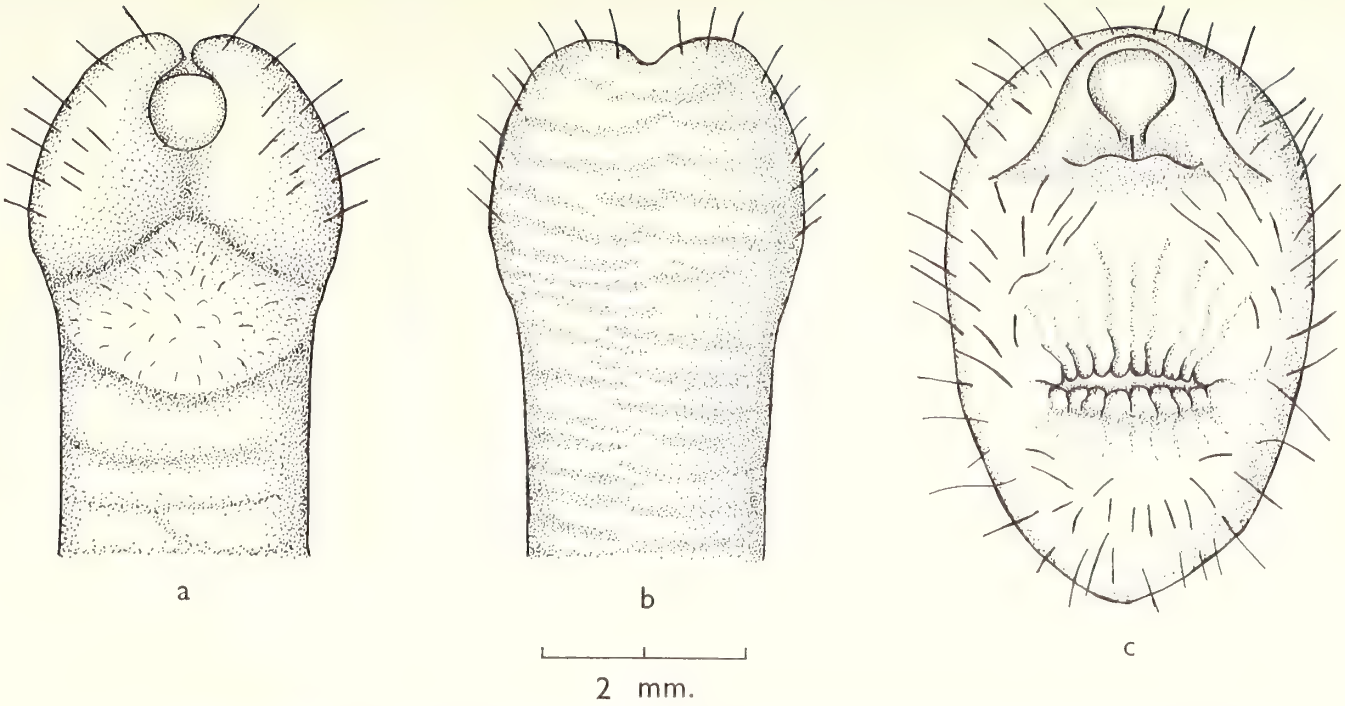

FIG. 3. *Pipistrellus joffrei.* *a*, dorsal aspect of penis ; *b*, ventral aspect of penis ; *c*, female external genitalia.

of its width. There seems little doubt from the description by Tate (1942 : 252) that *Pipistrellus anthonyi* is very closely related to *P. joffrei*, differing from this species only in colour and in minor cranial details. It appears to be known only from the male holotype, a dry skin with damaged skull, and no details of the external genitalia are available. The description and measurements suggest that it may approach even more closely to *Philetor* than does *Pipistrellus joffrei* in the widening of the rostrum, the degree of development of the supraorbital tubercles and the extent of the shortening of $\mathrm{pm}\frac{4}{4}$.

The remaining species allocated to the *joffrei* group seem much less closely related to *Philetor* than are *Pipistrellus joffrei* or *P. anthonyi*. The ears and tragus of *P. stenopterus* are similar to those of *P. joffrei* but the wing is less reduced with the fifth digit less shortened, its metacarpal nearly as long as the metacarpal of the fourth digit and its tip reaching almost to the distal end of the first phalange of the fourth digit. The penis, although about the same length as in *P. joffrei*, lacks any rudimentary pad on the dorsal surface of its shaft and there is no preputial fold. It consists instead of a simple shaft with a median longitudinal fissure along its dorsal surface extending to a terminal opening. The female external genitalia are similar to those of *P. joffrei*. The skull is much like that of *P. joffrei* but the supraorbital tubercles are less developed. The anterior upper premolar (pm^2) is relatively larger than in *P. joffrei* and pm_2 is unreduced, its height equal to that of pm_4, which it exceeds in both length and width. The crown area of pm_2 is twice that of pm_4, which is more reduced than in *P. joffrei*. From the description by Tate (1942 : 253) based on an alleged " co-type ", *Pipistrellus brachypterus* seems very near to *P. stenopterus*, and, if the specimen described by Dobson (1876 : 92, 1878 : 223) from the Berlin Museum is correctly identified as *brachypterus*, then possibly these are conspecific or even synonymous. Of particular significance is the remark by Dobson concerning the Berlin specimen that its first lower premolar (pm_2) is slightly longer than and in transverse diameter nearly double the second (pm_4) and is also nearly equal to the canine in vertical extent.

The Vespertilioninae comprise a complex of closely interrelated genera separated in some instances by comparatively slender or even rather arbitrary distinctions and the pattern of relationship within the subfamily is often obscured by parallelism or convergence. However, there is substantial evidence to indicate a relationship between *Philetor* and the *joffrei* group of *Pipistrellus* and also between *Philetor* and *Tylonycteris*, although *Philetor* seems sufficiently removed from both *Pipistrellus* and *Tylonycteris* to justify its retention as a distinct genus, presenting as it does a combination of features not met with elsewhere. In a suggested phylogeny of the pipistrelloid genera, Tate (1942 : 233, fig.) derived *Philetor, Tylonycteris* and *Mimetillus* from a point on the *Pipistrellus* stem. I would endorse the view expressed by this author elsewhere in the same paper (p. 266) that *Philetor* and *Tylonycteris* are derived from near the *Pipistrellus joffrei* group and have lost the small pm^2 independently. In a number of respects the two genera display further extensions of trends evidently inherent in this group : in *Philetor* the external genitalia have become very much modified and *Tylonycteris* has developed additional specializations of the thumbs, feet and braincase. There seems little doubt that *Philetor* and *Tylonycteris* are closely related but the affinities of *Mimetillus* are less certain. Although in some features it approaches *Philetor* and *Tylonycteris*, in others it differs markedly from both genera and, if not an indication of independent origin, these characteristics suggest no more than a remote relationship. The exact status of the *joffrei* group is open to some doubt. As Tate (1942 : 252) suggests, it may warrant subgeneric recognition within *Pipistrellus* but it has not been possible to examine all of the species allocated to it and until this can be done its status must remain uncertain. There is insufficient evidence to justify its transfer to *Philetor* and in any event, only *joffrei* and *anthonyi* among its included species show any near approach to that genus.

SUMMARY

The genus *Philetor* is considered to remain monotypic but two subspecies of *P. rohui* are now recognized, the nominate subspecies being so far known only from New Guinea. *Eptesicus verecundus* Chasen, 1940, from Malaya, is not an *Eptesicus* but is referable to *Philetor*. It is very similar to specimens from New Guinea and is allocated to *P. rohui* as the second subspecies. A review of the structural features of *Philetor* and of other genera and species to which relationship has been postulated hitherto indicates that its affinities are with the *joffrei* group of *Pipistrellus* and with the genus *Tylonycteris*.

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PONTOBDELLINAE (PISCICOLIDAE : HIRUDINEA)

IN THE BRITISH MUSEUM (NATURAL HISTORY) WITH A REVIEW OF THE SUBFAMILY

L. C. LLEWELLYN

BULLETIN OF
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BY

By L. C. LLEWELLYN

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SYNOPSIS

The conspicuously tuberculate marine leeches may conveniently be separated in a new subfamily Pontobdellinae containing the genera *Stibarobdella*, *Pontobdella*, and *Pentabdella* gen. nov., for species in which the mid-body somites bear three†, four and five annuli respectively.

The internal anatomy of *Stibarobdella macrothela* is described and is found to be similar to that of *Pontobdella muricata*, except that the former has a somewhat longer proboscis, a pair of lateral diverticula near the origin of the caecum, traces of caecal fenestrae, more elongated

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† or no more than three (p. 439).

seminal vesicles and ovaries and the abdominal ganglia less widely separated from one another. The extra annulus in each abdominal somite of Pontobdella seems to be innervated from the ganglion anterior to it.

Of the *Stibarobdella* examined, *S. macrothela* is particularly characterized by a very large posterior sucker, amorphous tubercles with large, more or less square basal areas and a pair of ocular patches ; *S. loricata* by a large anterior sucker with a fringe ; *S. bimaculata* by small suckers and tubercles and a pair of ocular patches ; and *S. variegata* by a mid-ventral tubercle on each a_2 annulus.

Of the *Pontobdella* examined, *P. muricata* is distinguished by a large anterior sucker with a fringe and *P. vosmaeri* by a small anterior sucker lacking a fringe and by a mid-ventral tubercle on each a_2 annulus.

Complete descriptions of external characters are given for these species, all the literature relating to the Pontobdellinae is reviewed and attention is drawn to a number of *species inquirendae*. A key is constructed for the identification of the species reviewed.

INTRODUCTION

THE group of closely related Piscicolid marine leeches, which are characterized by possessing numerous tubercles on each body somite, are often placed in the single genus *Pontobdella* Leach. Many of the descriptions of these leeches are inadequate or based on characters which vary individually in those species which have been more thoroughly studied. The literature about them is scattered and needs reviewing. In the absence of convenient works of identification, the British species are not well known. Examination of material in the collection of the Plymouth Laboratory, for instance, revealed the presence of two species, preserved together under the same name, *Pontobdella muricata* (L.), the second, previously unrecognized species being *Pontobdella vosmaeri* Apathy.

A preliminary examination of fifty specimens of *Pontobdella muricata*, the most examined from one species, showed that the characters of the suckers were a reliable guide to identification. Papillation and relative size always appeared to be reasonably constant, though slight variations in size due to contraction obviously had to be taken into account. The number of annuli in the clitellar constriction, however, may be cited as an example of a character which occasionally varies slightly. The number and distribution of the smaller tubercles is also variable, particularly on the smaller annuli. Some of the specimens examined appeared to be rather starved and contracted, having a slender anterior region separated by the clitellum from a broad, flattened posterior region. These unsatisfactory characters were used by Harding (1927) as diagnostic of the subgenus *Pontobdellina*, which he erected for the single species *Pontobdella macrothela* Schmarda.

Harant (1929), too, proposed a questionable new genus *Parapontobdella*, for *Pontobdella tatejamensis*, which was described rather briefly by Oka (1910). He separated it on the grounds that it was said to possess some indication of lateral vesicles. According to Selensky (1915), however, it is quite usual for a species of *Pontobdella* to show a few somewhat inconspicuous vesicles, so although there are insufficient reasons for retaining *tatejamensis* in *Pontobdella* (see p. 436), *Parapontobdella* may have to be separated on other characters.

As my studies progressed it became evident that one set of characters, which was always constant in any species, was the number of annuli per somite. This seems important because, in the past, closely related Piscicolidae, such as *Piscicola* and *Calliobdella*, have been divided on the basis of the number of annuli per somite, together with secondary differences. It is convenient, therefore, to use a similar criterion of classification for those species usually assigned to *Pontobdella*. All the species in this group are either, tri-, tetra- or pentameric, i.e. each somite of the testicular and caecal (blind-gut) regions is composed of three, four or five annuli respectively. The additional annuli per somite necessitate modification of the nervous system to innervate them. I propose, therefore, to follow Harant (1929) in restricting *Pontobdella*, to include only tetrameric species, and redefining *Stibarobdella*, to include all trimeric species, and to name a third genus for the only known pentameric species. The three genera can then be placed conveniently in a new subfamily, the Pontobdellinae, when the new classification becomes as follows :—

Subfamily **Pontobdellinae**

Genus ***Stibarobdella*** Leigh-Sharpe, 1925, for trimeric species (but see p. 439)
Genus ***Pontobdella*** Leach, 1815, for tetrameric species
Genus ***Pentabdella*** gen. nov., for pentameric species

The sections which follow aim to give : 1. An introduction to the internal anatomy of these forms by comparing dissections of the type species of the genera *Stibarobdella* and *Pontobdella*. 2. A systematic account of the genera and species placed in the sub-family, accompanied by details of several *species inquirendae*.

MATERIAL

About seventy-five specimens in the British Museum (Natural History) were examined and about twenty-five from Plymouth. They comprised seven species, two of which occur at Plymouth. The number examined of a particular species is given later, at the beginning of the description of the species.

ANATOMICAL COMPARISON OF *STIBAROBDELLA MACROTHELA* AND *PONTOBDELLA MURICATA*

The internal anatomy of *Pontobdella muricata* is fairly well known from the work of Bourne (1884), Vaillant (1870) and Leydig (1851), but that of *Stibarobdella macrothela* is hardly known at all. The general dissections depicted in Text-figs. 1 and 2 show the relationship of the organs to the somites of the body. The following description applies to both species unless stated otherwise.

Gut. The proboscis in *Pontobdella muricata* extends from somite VII to the middle of somite IX, while in *Stibarobdella macrothela* it extends from somite VII into the anterior part of somite X, at least a specific taxonomic difference according to Selensky (1915). Clearly visible protractor muscles are attached to the posterior end of the proboscis sheath. Along each side of the oesophagus and pharynx lie salivary glands which penetrate the proboscis at its base. The oesophagus is short and its precise limits are difficult to determine. The anterior portion of the intestine,

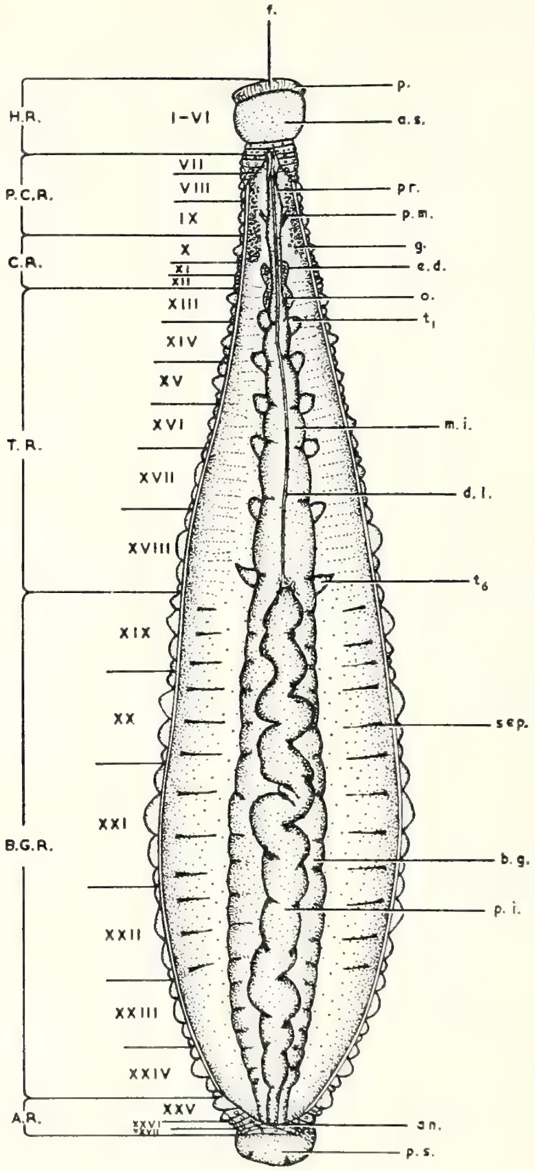

f.
p.
H.R.
I–VI
a.s.
VII
P.C.R.
VIII
pr.
IX
p.m.
g.
X
C.R.
XI
e.d.
XII
XIII
o.
t_1
XIV
XV
XVI
m.i.
T.R.
XVII
d.l.
XVIII
t_6
XIX
XX
sep.
XXI
B.G.R.
b.g.
p.i.
XXII
XXIII
XXIV
XXV
A.R.
XXVI
XXVII
an.
p.s.

Fig. 1. General dissection of *Pontobdella muricata* to show relationship of organs to somites of the body. I–XXVII, numbering of somites; *an.*, anus; A.R., anal region; *a.s.*, anterior sucker; *b.g.*, caecum (blind-gut); B.G.R., caecal region (blind-gut region); C.R., clitellar region; *d.l.*, dorsal blood vessel; *e.d.*, ejaculatory duct; *f.*, fringe; *g.*, salivary gland cells; H.R., head region; *m.i.*, mid-intestine; *o.*, ovary; *p.*, papilla; P.C.R., pre-clitellar region; *p.i.*, posterior intestine; *p.m.*, protractor muscle; *pr.*, proboscis; *p.s.*, posterior sucker; *sep.*, septa; t_1–t_6, testes; *T.R.*, testicular region.

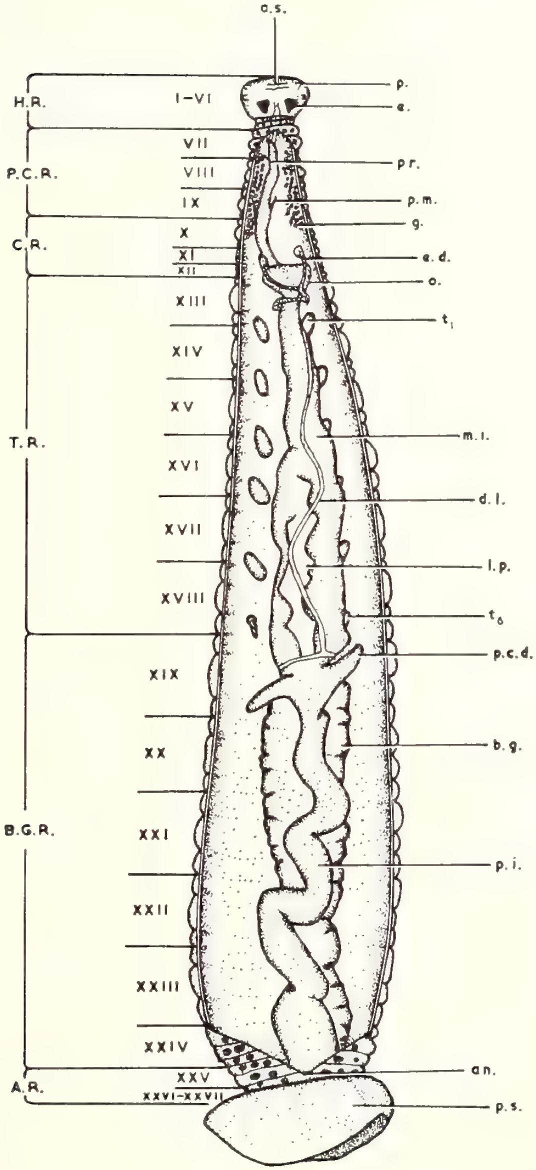

a.s.
p.
e.
pr.
p.m.
g.
e.d.
o.
t_1
m.i.
d.i.
l.p.
t_6
p.c.d.
b.g.
p.i.
an.
p.s.
H.R.
P.C.R.
C.R.
T.R.
B.G.R.
A.R.
I–VI
VII
VIII
IX
X
XI
XII
XIII
XIV
XV
XVI
XVII
XVIII
XIX
XX
XXI
XXII
XXIII
XXIV
XXV
XXVI–XXVII

FIG. 2. General dissection of *Stibarobdella macrothela* to show relationship of organs to somites of the body. *e.*, pigmented eye patches ; *l.p.*, lateral projections of mid-intestine ; *p.c.d.*, diverticula. See Fig. 1 (p. 394) for other abbreviations.

which stretches from the posterior edge of the oesophagus to the XIIth or last clitellar somite, is fairly thick-walled in *Stibarobdella,* while it appeared to be more membranous in *Pontobdella.* A very small pair of diverticula come out from the gut in somite XI, though Selensky (1915) found these in somite X. It should be noted that Selensky in fact called this somite VIII, but believed the head complex to contain four somites ; it is now regarded as containing six somites (Mann, 1953), so appropriate amendments are made here and throughout the text following.

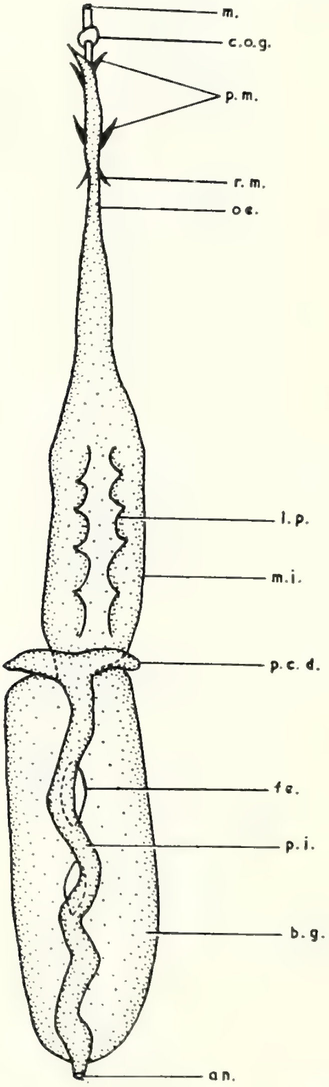


FIG. 3. Gut of *Stibarobdella macrothela : c.o.g.,* circum-oesophageal ganglion ; *fe.,* fenestra ; *m.,* mouth ; *oe.,* oesophagus ; *r.m.,* retractor muscle. See Figs. 1 & 2 (p. 394 & p. 395) for other abbreviations.

The mid-intestine, which extends throughout the testicular region, is divided by constrictions into six chambers in *Pontobdella muricata*, corresponding to the six somites (XIII to XVIII) of this region. In *Stibarobdella macrothela* there are instead small lateral projections on the dorsal surface of the mid-intestine (Text-fig. 3). From the posterior end of the mid-intestine arises the caecum, which in *Pontobdella* is entirely unpaired and extends ventrally from somites XVIII to XXVI. In *Stibarobdella* it extends from somites XIX to XXVI and shows signs of fenestrae in somites XX and XXII, although these were not particularly clear and seem unimportant in distinguishing genera. Selensky (1915) regarded the degree of fusion of caeca as generally constant within a genus, but Moore (1938) found in *Pontobdella rugosa* that the last pair of caeca are only partially fused with five fenestrae. The caecum in *Pontobdella muricata* shows slight constrictions corresponding to the increased musculature or rudimentary septa found between annuli a_1–a_2, a_2–b_5 and within the small annulus b_6, but these cannot easily be distinguished in *Stibarobdella macrothela*. The labelling of annuli is explained by Mann (1953) and can be seen in Text-fig. 9 (p. 403).

The posterior intestine extends from somites XIX to XXVII and is surrounded for most of its length by a blood sinus, which anterior to this forms the dorsal blood vessel. In *Stibarobdella macrothela* there is a large pair of diverticula in somite XIX, but in *Pontobdella muricata* there is only a slight swelling here. Beyond this the intestine winds backwards. Numerous septa occur within it, but these are not obvious from the exterior. Finally, the rectum is short and rather inconspicuous and terminates at the anus between somites XXVI and XXVII, or in *Pontobdella muricata* between the annuli of somite XXVI, or in the anterior annulus of this somite.

Reproductive system. Both species possess six pairs of oval testes (Text-figs. 4 and 5), situated posteriorly in somites XIII to XVIII. When fully ripe each overlaps into the somite behind, becoming virtually intersegmental. Richardson (1950) described *Pontobdella benhami* (=*Stibarobdella macrothela*) as having three pairs of testes and according to his diagram the vas deferens looped posteriorly for another two somites after the posterior testes. It seems, however, that it is quite possible for this leech to possess six pairs of testes, as is normal in Piscicolidae. In *Pontobdella muricata* each of the vasa efferentia leaves the testis antero-laterally, while in *Stibarobdella macrothela* it leaves postero-ventrally. This character, however, may perhaps vary with contraction and during the ontogeny. The vasa efferentia proceed laterally to join the vas deferens on each side. This proceeds anteriorly, following a more wavy course in *Pontobdella muricata*, and joins the ejaculatory duct in somite XI in this form, but in somite XII in *Stibarobdella macrothela*. The ejaculatory duct communicates posteriorly with a long coiled vesicula seminalis and extends anteriorly as far as somite XI, where it coils postero-ventrally and finally enters the dorsal portion of the genital atrium, which is divided dorso-laterally into two pouches. The male pore opens in somite XI, between the second and third annulus in *Pontobdella muricata*, and between the two annuli of this somite in *Stibarobdella macrothela*.

The paired ovaries are tubular but comparatively short, leading into short oviducts

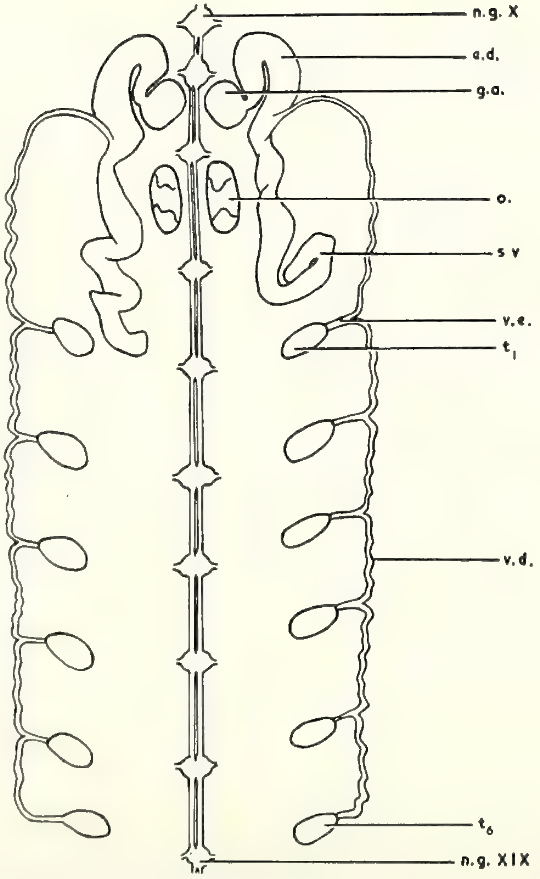

n.g. X
e.d.
g.a.
o.
s v
v.e.
t_1
v.d.
t_6
n.g. XIX

FIG. 4

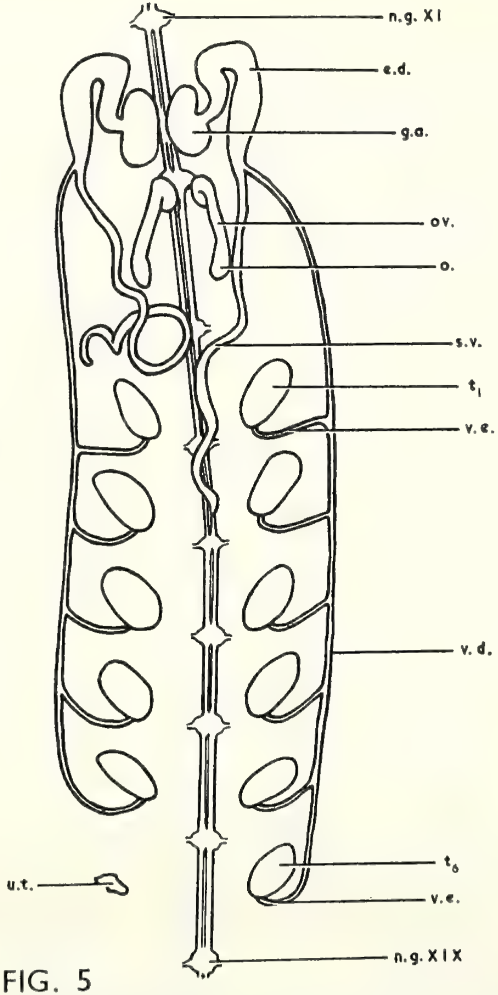

n.g. XI
e.d.
g.a.
ov.
o.
s.v.
t_1
v.e.
v.d.
t_6
v.e.
u.t.
n.g. XIX

FIG. 5

FIGS. 4, 5. Fig. 4. Reproductive system of *Pontobdella muricata*. *e.d.*, ejaculatory duct; *g.a.*, genital atrium; *n.g. X–XIX*, nerve ganglia of somites X–XIX; *o.*, ovary; *s.v.*, vesicula seminalis; t_1–t_6, testes; *v.d.*, vas deferens; *v.e.*, vas efferens. Fig. 5. Reproductive system of *Stibarobdella macrothela*. *ov.*, oviduct; *u.t.*, undeveloped testis. See Fig. 4, p. 398, for other abbreviations.

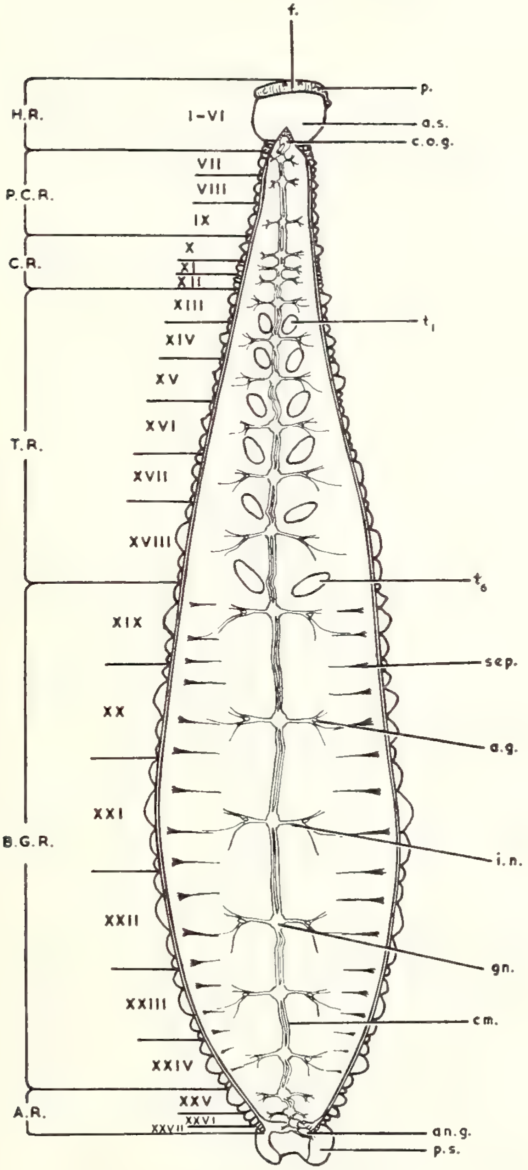

f.
H.R.
I–VI
p.
a.s.
c.o.g.
VII
VIII
P.C.R.
IX
X
C.R.
XI
XII
XIII
t_1
XIV
XV
XVI
T.R.
XVII
XVIII
t_6
XIX
sep.
XX
a.g.
XXI
B.G.R.
i.n.
XXII
gn.
XXIII
cm.
XXIV
XXV
A.R.
XXVI
XXVII
an.g.
p.s.

FIG. 6. Dissection to show the arrangement of ganglia in the neurosomites of *Pontobdella muricata*. *a.g.*, accessory ganglion (or lateral glia cells); *an.g.*, anal ganglion; A.R., anal region; *a.s.* anterior sucker; B.G.R., caecal region (blind-gut); *cm.*, commissure; *c.o.g.*, circum-oesophageal ganglion; C.R., clitellar region; *f.*, fringe; *gn.*, ganglion; H.R., head region; *i.n.*, segmental nerve; *p.*, papilla; P.C.R., preclitellar region; *p.s.*, posterior sucker; *sep.*, septa; t_1–t_6, testes; T.R., testicular region.

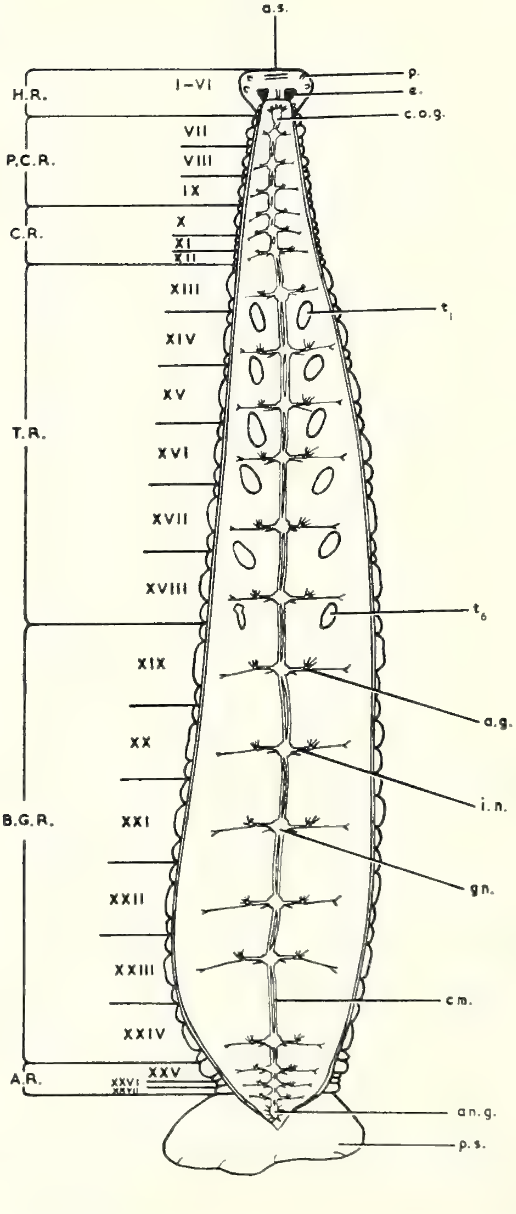

a.s.
p.
e.
c.o.g.
H.R.
I–VI
VII
P.C.R.
VIII
IX
C.R.
X
XI
XII
XIII
t_1
XIV
XV
T.R.
XVI
XVII
XVIII
t_6
XIX
a.g.
XX
i.n.
B.G.R.
XXI
gn.
XXII
XXIII
c.m.
XXIV
A.R.
XXV
XXVI
XXVII
an.g.
p.s.

FIG. 7. Dissection to show the arrangement of ganglia in the neurosomites of *Stibarobdella macrothela*. *e.*, pigmented eye patches. See Fig. 6 (p. 399) for other abbreviations.

which terminate in the female pore, between the two annuli of somite XII in *Stibarobdella macrothela*, and between the first and second annulus of somite XII in *Pontobdella muricata*.

NERVOUS SYSTEM AND ANNULATION. Between the circum-oesophageal and anal ganglionic masses, lie twenty-one ganglia joined by commissures, which mark a corresponding number of somites (Text-figs. 6 and 7). These are grouped by Johansson (1896) and others as follows :—

Preclitellar region	3
Clitellar region	3
Testicular region	6
Caecal (blind-gut) region	6
Anal region	3

Following Mann (1953), we may provisionally assume that the circum-oesophageal mass consists of six neurosomites, in spite of older views that it consists of four (Livanow, 1903 and 1904, and others). In *Pontobdella muricata* it innervates the anterior sucker plus the adjoining three narrow annuli, which together constitute the head region. The widths of these three annuli are in the ratio 1 : 1 : 2. In *Stibarobdella macrothela* the arrangement of the head region is very similar, except that occasionally only two neck annuli can be distinguished.

In both species, the next three neuro-somites of the preclitellar region VII–IX are trimeric, with their annular widths varying in the ratio 1 : 2 : 1. The anterior limit of the clitellar region is rather ambiguous in all Pontobdellinae. The most obvious external clue to the position of the clitellum is a constriction of the body and a reduction in width of the annuli there. The size and number of tubercles are also reduced. The most anterior of these narrow annuli is the last annulus of somite X and the most posterior is the first annulus of somite XIII. The term " clitellar region " generally given to the three somites X–XII does not therefore coincide exactly with the narrow and modified part of the body.

Posterior to the clitellar region lies the testicular region which is made up of six somites, XIII to XVIII. In *Stibarobdella macrothela* these are trimeric, with their widths varying in the ratio 1 : 2 : 1, while in *Pontobdella muricata* they are tetrameric with their widths varying in the ratio 2 : 3 : 2 : 1. The ganglia always appear to be situated within the limits of the largest annulus. Behind this region lies the caecal region, which is also made up of six somites XIX to XXIV, having an arrangement similar to that in the previous region.

The anal region is made up of three somites, XXV to XXVII, containing three ganglia which are much closer together. In *Stibarobdella macrothela* somite XXV consists of two annuli and XXVI and XXVII of one annulus each. Finally, the posterior ganglionic mass of the posterior sucker is regarded as consisting of seven fused ganglia, making a total of thirty-four in all.

The distance between ganglia varies considerably and is least towards the extremities of the nerve chain and in the clitellar region (Text-fig. 8). In *Pontobdella* *muricata* the distance between ganglia in the caecal region is relatively greater than in *Stibarobdella macrothela*.

Each ganglion consists of ganglia cells arranged into six cell packets or capsules, with one pair on each side and one pair mid-ventrally, making three longitudinal rows. Through the middle of the ganglion run two fibrous tracts, which fuse at the centre of the ganglion (Harant & Grassé, 1959) and continue as the commissures linking successive ganglia, each tract possessing a single " commissural cell " making a total of two between adjacent ganglia. From the fibrous tract at the centre of the ganglion the main segmental nerve runs out on each side. In *Pontobdella muri-*

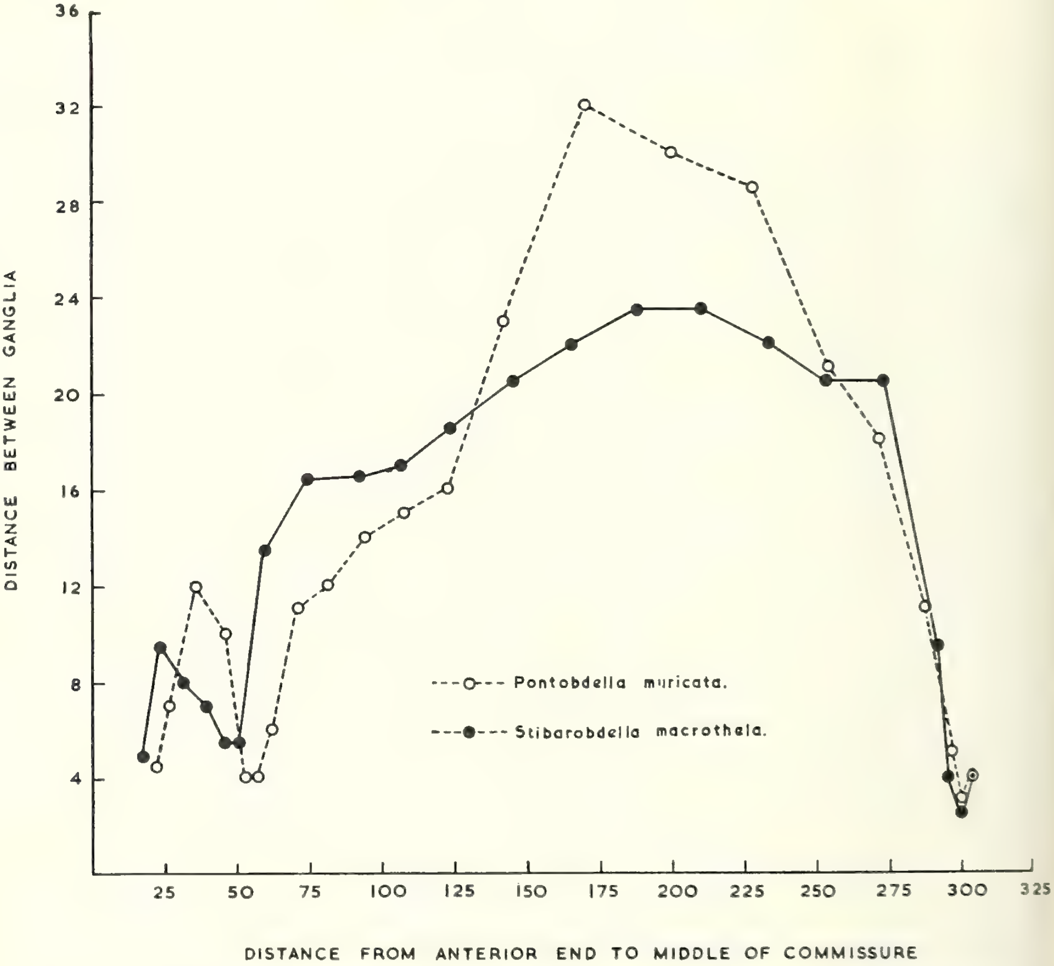


FIG. 8. Graph to show relative distances between ganglia in *Pontobdella muricata* and *Stibarobdella macrothela* and the elongation of the caecal (blind-gut) region in the former. The scales for the axis and abscissa are in arbitrary units which differ slightly between species. The measurements were taken from one specimen of each species.

FIG. 9

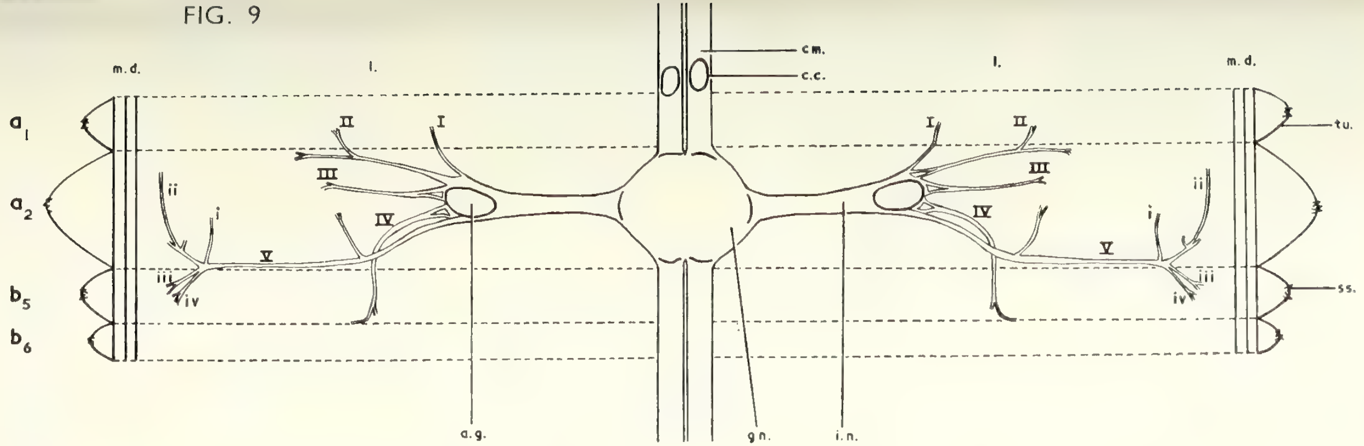
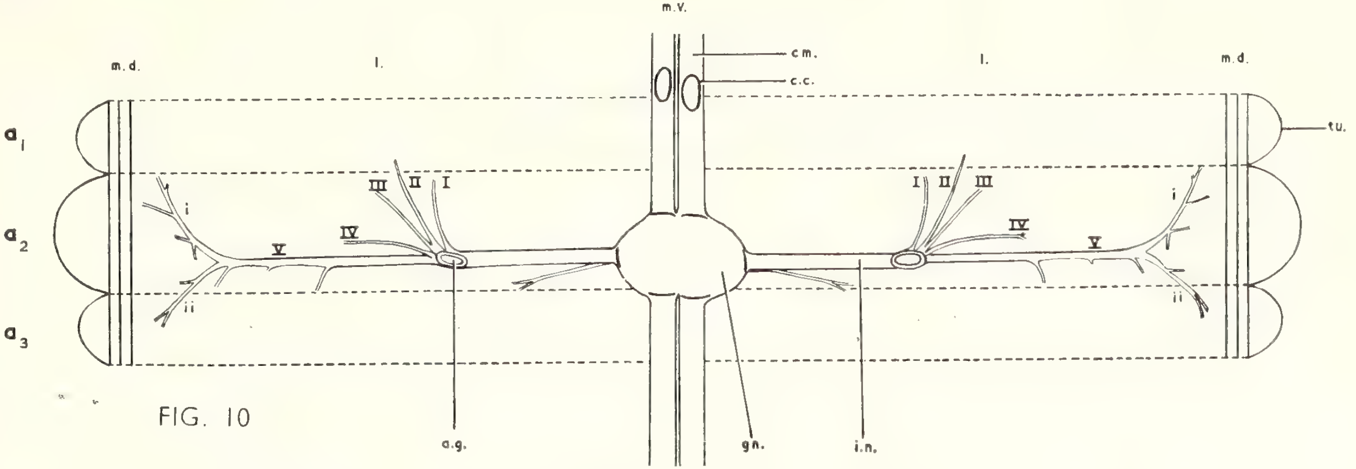

m.d.
l.
c.m.
c.c.
l.
m.d.
a1
a2
b5
b6
tu.
ss.
I
II
III
IV
V
i
ii
iii
iv
a.g.
gn.
i.n.

FIG. 10


m.v.
m.d.
l.
c.m.
c.c.
l.
m.d.
a1
a2
a3
tu.
I
II
III
IV
V
i
ii
a.g.
gn.
i.n.

FIGS. 9, 10. Fig. 9. Neurosomite of *Pontobdella muricata* showing the main nerve branches. For designations of annuli (i.e. a_1, a_2, b_5 and b_6) see Mann, 1953. *a.g.*, accessory ganglion (or lateral glia cells); *c.c.*, commissural cell; *c.m.*, commissure; *gn.*, ganglion; *i.n.*, segmental nerve; *l.*, lateral line; *m.d.*, mid-dorsal line; *m.v.*, mid-ventral line; *ss.*, sensilla; *tu.*, tubercle. *I–V*, numbering of somitic nerves. *i–iv*, numbering of branches of nerve V. Fig. 10. Neurosomite of *Stibarobdella macrothela* showing the main nerve branches. For designations of annuli (i.e. a_1, a_2 and a_3) see Mann, 1953. *i–ii*, numbering of branches of nerve V. See Fig. 9 for other abbreviations.

cata, in the testicular and caecal region, this nerve divides near the lateral glia cells or accessory ganglia (Scriban & Autrum, 1934) into five main branches (Text-fig. 9). Nerve I, the most anterior branch, is comparatively small. It turns ventrally and innervates the ventral portion of annulus a_1. Nerve II curves anteriorly and innervates annulus a_1 laterally. Nerve III runs laterally and terminates in the lateral region of annulus a_2. Nerve IV runs laterally for a short distance and then posteriorly until it reaches the boundary between annulus b_5 and b_6. There it divides, the main branch turning laterally again and running along this boundary It seems likely that one of these nerve branches innervates annulus b_6. Nerve V, which is the largest of these nerves, runs along the boundary between annuli a_2 and b_5 until it subdivides dorso-laterally into four branches (i–iv), innervating the lateral and dorsal regions of annulus a_2 and b_5.

Stibarobdella macrothela differs from this condition in several ways (Text-fig. 10). The main segmental nerve trunk gives off a branch as it leaves the ganglion, which terminates ventrally in the region of the border between annulus a_2 and a_3. As in *Pontobdella muricata* there are five main branches at the lateral glia cells, of which I, II and III run anteriorly. Nerve IV appeared to terminate laterally in annulus a_2. The main branch, nerve V, had a small branch in the region of the lateral line, which ran posteriorly and terminated at the border between annulus a_2 and a_3. The main branch continued dorsally with two very small branches running posteriorly, until in the dorso-lateral region of annulus a_2 it divided, the posterior branch ii terminating in annulus a_3, the anterior branch i in annulus a_2.

It can be seen that the arrangement of nerves I, II, III and V is somewhat similar in the two species. Only nerve IV is strikingly different, being elongated posteriorly in *Pontobdella muricata* and apparently innervating annulus b_6. This supports the view put forward by Oka (1917), who stated that the fourth annulus of a tetrameric somite is derived from the a_3 annulus. It seems that annulus b_6 is indeed the posterior annulus of the somite and that the modifications are for the innervation of this fourth annulus.

Family **PISCICOLIDAE**

Subfamily **PONTOBDELLINAE**, Subfam. nov.

Diagnosis. Characterized particularly by the tubercles, which occur on at least the major (a_2) annulus of each somite and usually on most annuli of the testicular and caecal regions. The latter regions are divided into trimeric, tetrameric or pentameric somites. The body is circular or slightly flattened in cross section. The clitellar constriction does not coincide exactly with the three clitellar somites (X, XI, and XII) of the " clitellar region " defined by Johansson (1896) for most Hirudineae, but extends from Xa_3 to $XIIIa_1$ inclusive (Text-figs. 11–28).

Type genus. *Pontobdella* Leach, 1815.

Remarks. Pending further studies the remaining Piscicolidae should perhaps be grouped as the Piscicolinae and Branchelliinae (Caballero, 1956) and may eventually be divided further. Leigh-Sharp (1916) suggested that those possessing pulsatile vesicles or other respiratory appendages might be separated off as the Branchiobdellinae, but this name is unacceptable, since *Branchiobdella* is an oligochaete, and there are intermediate forms, such as *Johanssonia* and *Austrobdella*, which make such separation difficult.

Genus ***STIBAROBDELLA*** Leigh-Sharpe, 1925*

Stibarobdella Leigh-Sharpe, 1925 : 417 ; Harant, 1929 : 651.
Pontobdella (*Pontobdellina*) Harding, 1927 : 44.

TYPE SPECIES. *Pontobdella macrothela* Schmarda.

DIAGNOSIS. Somites of the testicular and caecal regions trimeric (but see p. 439)

Stibarobdella macrothela (Schmarda, 1861).

Pontobdella macrothela Schmarda, 1861 : 6.
Pontobdella afra Baird, 1869 : 312.
Pontobdella papillata Grube, 1871 : 56.
Pontobdella zonata Weber, 1915 : 20.
Pontobdella (*Pontobdellina*) *macrothela* : Harding, 1927 : 45.
Pontobdella benhami Richardson, 1950 : 97.
Trachelobdella carajbica Dequal, 1917 : 2.
Stibarobdella superba Leigh-Sharpe, 1925 : 417.

DESCRIPTION. *General characters.* About thirty specimens were examined. The testicular and caecal regions are somewhat flattened, except when fully gorged, and are distinctly broader than and clearly separated from those regions anterior to them. The body varies from yellowish brown to bluish green, even in preserved material, with the tubercles generally white or cream, and sometimes with bands or patches of pigment. The length may reach 16·5 cm., excluding suckers. The anterior sucker is slightly oval, elongated transversely and attached eccentrically, with the dorsal surface longer than the ventral. It lacks a marginal fringe (Text-fig. 11A and 12), but possesses three pairs of tentacular papillae situated marginally and one pair laterally nearer the base of the sucker. These are occasionally rather difficult to see. All specimens examined had coronet-shaped (ocular?) pigment patches on the dorsal surface of the anterior sucker, although in one long preserved specimen these had become extremely faint. The posterior sucker, which is attached centrally, is between two and three times the size of the anterior sucker and is generally almost twice the diameter of its attachment and broader than the broadest part of the body. When contracted, however, it may be little more than half the greatest breadth of a fully gorged specimen. Sometimes it bears dark and light radiating bands or patches.

ANNULATION.	Uniannulate somites		XXV, XXVI	XXVII
	Biannulate somites	XI, XII		
	Triannulate somites	VII–X, XIII–XXIV		(Text-fig. 12)

The first three annuli of the body, the anterior two of which are particularly narrow, constitute the neck, which together with the anterior sucker makes up the

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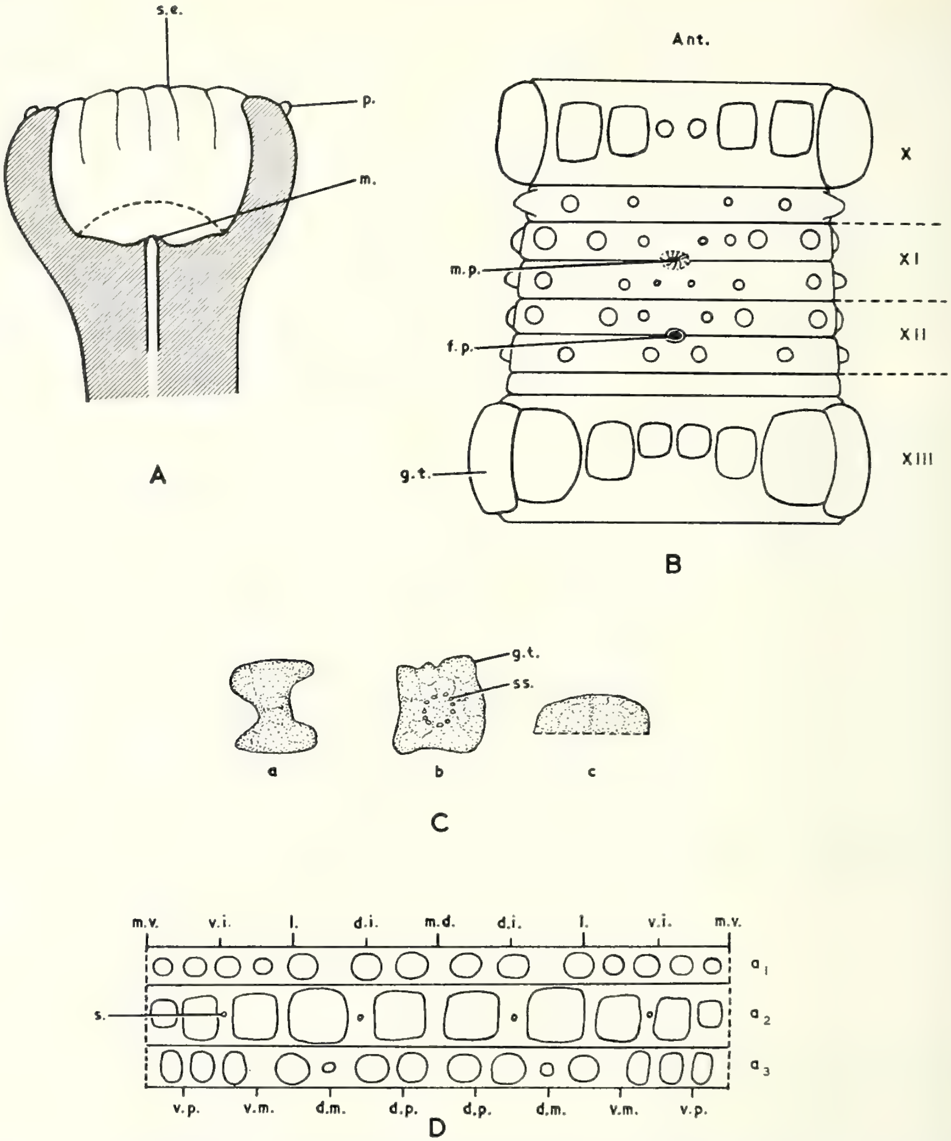
* Including *Stibarobdella biannulata* (Moore), see p. 439


s.e.
p.
m.
A
Ant.
X
XI
m.p.
XII
f.p.
XIII
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B
g.t.
ss.
a
b
c
C
m.v.
v.i.
l.
d.i.
m.d.
d.i.
l.
v.i.
m.v.
a_1
s.
a_2
a_3
v.p.
v.m.
d.m.
d.p.
d.p.
d.m.
v.m.
v.p.
D

FIG. 11. *Stibarobdella macrothela.* A. Section through anterior sucker, showing oral surface. B. Ventral surface of clitellar constriction, showing positions of genital pores and tubercles. C. (a, b and c). Glandular or furrowed tubercles. D. Tuberculation of a typical triannulate somite split mid-ventrally. For designations of annuli (i.e. a_1, a_2 and a_3) see Mann, 1953. *X–XIII*, numbering of somites; *Ant.*, anterior end; *d.i.*, dorsal intermediate line; *d.m.*, dorso-para-marginal line; *d.p.*, dorso-para-median line; *f.p.*, female pore; *g.t.*, furrowed tubercle; *l.*, lateral line; *m.*, mouth; *m.d.*, mid-dorsal line; *m.p.*, male pore; *m.v.*, mid-ventral line; *p.*, papilla; *s.e.*, scalloped edge; *ss.*, sensilla; *v.i.*, ventral intermediate line; *v.m.*, ventro-para-marginal line; *v.p.*, ventro-para-median line.

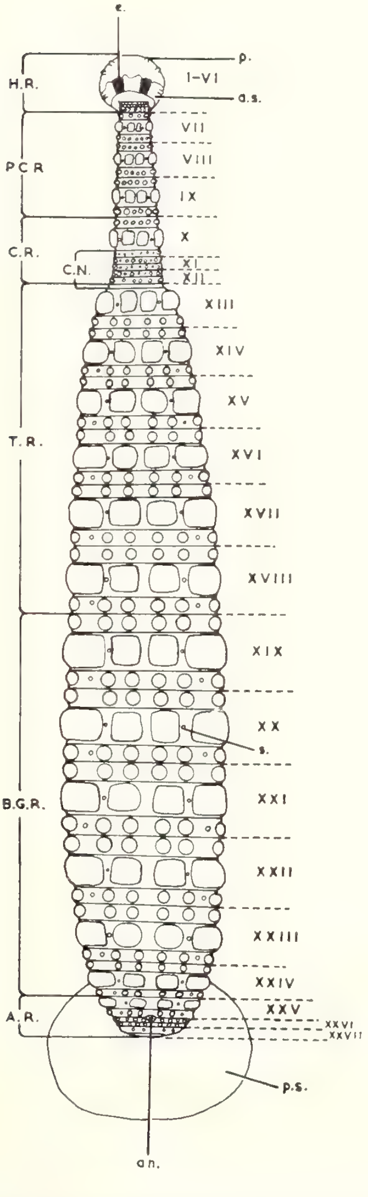

e.
p.
H.R.
I–VI
a.s.
VII
PCR
VIII
IX
X
C.R.
C.N.
XI
XII
XIII
XIV
XV
T.R.
XVI
XVII
XVIII
XIX
XX
s.
B.G.R.
XXI
XXII
XXIII
XXIV
A.R.
XXV
XXVI
XXVII
p.s.
an.

FIG. 12. Dorsal view of *Stibarobdella macrothela* showing annulation, tuberculation and suckers. *I–XXVII*, numbering of somites; *an.*, anus; A.R., anal region; *a.s.*, anterior sucker; B.G.R., caecal region (blind-gut region); C.N., clitellar constriction; C.R., clitellar region; *e.*, pigment eye patches; H.R., head region; *p.*, papilla; P.C.R., pre-clitellar region; *p.s.*, posterior sucker; *s.*, small white tubercle; T.R., testicular region.

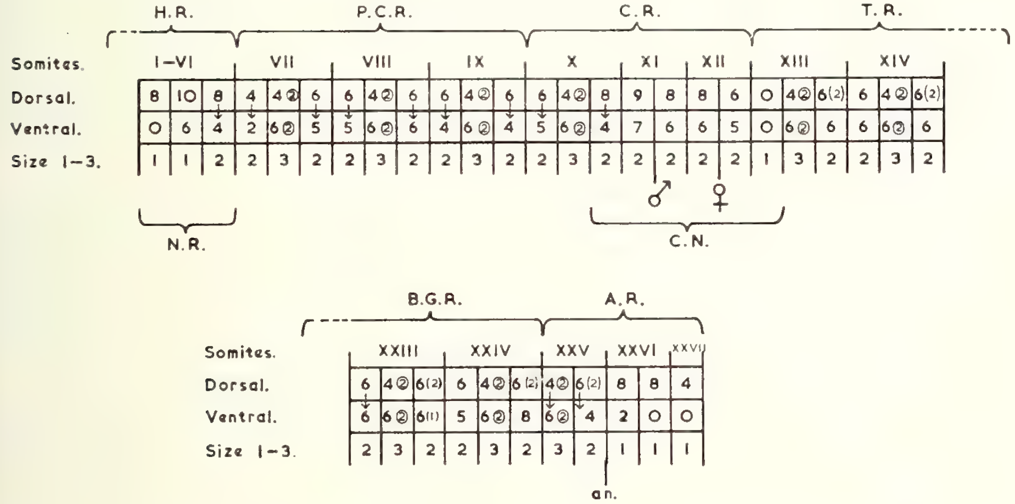
head region. Then come three trimeric somites forming the "preclitellar region". As already remarked (page 401) most of the first somite of the "clitellar region" also lies anterior to the clitellar constriction, which extends from Xa_3 to $XIIIa_1$. The male and female pores open on the ventral side of this constriction, between the two annuli of somites XI and XII respectively (Text-fig. 11B). In some specimens the male pore is surrounded by tumid lips. Annulus $XIIIa_1$ is extremely small and generally lacks tubercles, whilst the other annuli of the clitellar constriction are also rather small, of uniform size, and with tubercles of reduced size. Sometimes an annulus is absent from the posterior part of the clitellar constriction and this is probably annulus $XIIIa_1$, rather than one of the annuli of somite XII. If so, it appears that the first testicular somite XIII is then bi-annulate. The remaining five somites of the testicular region XIV to XVIII and the six of the caecal region XIX to XXIV are all trimeric and their annular widths vary in the ratio 2 : 3–4 : 2. The annulation and tuberculation of the anal region XXV to XXVII are subject to variation. The anus is situated in the furrow between somites XXV and XXVI. These are biannulate, whilst somite XXVII is usually uniannulate, but occasionally shows signs of becoming biannulate, as also observed by Cordero (1937–38). Moore (1927) described similar annulation in this region, but later (1958) described a further specimen with somite XXIV biannulate and XXV, XXVI and XXVII uniannulate. In all other respects annulation is generally the same as that described by Cordero (1937–38) and Moore (1927 and 1958).

TUBERCULATION. Text-fig. 13 illustrates the tuberculation of a single specimen. There is considerable individual variation, particularly affecting the smaller tubercles. The big tubercles, however, are fairly constant in number and arrangement. The tubercles on the first two annuli of the neck, which are minute, are often absent ventrally. On the ventral surface of the a_1 and a_3 annuli of the preclitellar region the number of tubercles varied from 4 to 7. Where odd numbers are indicated in Text-fig. 13, this was due to bilateral asymmetry and not to median tubercles. Somite XXVI and XXVII appear to have no sensillae or small white tubercles, and their annuli have more tubercles dorsally and few or none ventrally.

Text-fig. 11D shows a typical triannulate somite of the testicular or caecal region. Here and generally throughout the body, the dorsal tubercles are larger than the ventral ones. Numbers and sizes of tubercles are reduced towards the extremities of the body. These vary considerably in shape and size depending on extent of gorging, but the four large tubercles on the dorsal surface of the a_2 annuli differ from those of any other species examined (Text-figs. 11C*a*, *b* and *c*). They are generally more or less square, occasionally with lateral indentations making them somewhat "H" shaped (Text-fig. 11C*a*). They generally appear rather like cotton wool in texture and somewhat furrowed, and sometimes bear an apical ring of small sensillae.

In addition to these large tubercles there are generally four small white tubercles without papillae, which are difficult to see in starved specimens, two situated dorsolaterally and two ventro-laterally. The tubercles of a_1 and a_3 are generally more rounded and more like tubercles of other Pontobdellinae, although they too may possess rather irregular surfaces and small apical sensillae. The tubercles on the clitellar constriction are very small and rounded. Annulus XIIIa$_1$ lacks tubercles, but the other annuli of the clitellar constriction may possess up to eight both dorsally and ventrally. The size, position and number of these vary considerably.

REMARKS. *Hirudo indica* Linnaeus (=*Pontobdella indica:* de Blainville, 1827) may well have been this species (Harding, 1927). According to Cordero (1937–38) *Pontobdella moorei, Pontobdella bimaculata, Pontobdella zonata* and *Trachelobdella carajbica* are synonymous with *Pontobdella macrothela.* However, Oka (1929), in his comparison of the external morphology of *P. moorei, P. bimaculata* and *Pontobdella muricata,* never mentioned irregularly shaped tubercles, and these are known to be absent from *P. muricata* and were not illustrated in the diagrams of his other two species. Furthermore Cordero's view appears to require an undue degree of variation



Somites.	I–VI			VII			VIII			IX			X			XI		XII		XIII			XIV		
Dorsal.	8	10	8↓	4↓	4②	6↓	6↓	4②	6↓	6↓	4②	6↓	6↓	4②	8↓	9	8	8	6	0	4②	6(2)	6	4②	6(2)
Ventral.	0	6	4	2	6②	5	5	6②	6	4	6②	4	5	6②	4	7	6	6	5	0	6②	6	6	6②	6
Size 1–3.	1	1	2	2	3	2	2	3	2	2	3	2	2	3	2	2	2	2	2	1	3	2	2	3	2

Somites.	XXIII			XXIV			XXV		XXVI		XXVII
Dorsal.	6↓	4②	6(2)	6	4②	6(2)	4②↓	6(2)↓	8	8	4
Ventral.	6	6②	6(1)	5	6②	8	6②	4	2	0	0
Size 1–3.	2	3	2	2	3	2	3	2	1	1	1

FIG. 13. Diagram illustrating the tuberculation of a single specimen of *Stibarobdella macrothela.* The anterior half is shown above, reading from left to right, H.R., head region; P.C.R., preclitellar region; C.R., clitellar region; T.R., testicular region showing first two somites; N.R., neck region; C.N., clitellar constriction where ♂ and ♀ show the position of the respective pores. The posterior half is shown below including, reading from left to right, B.G.R., caecal region (blind-gut region); A.R., anal region; *an.*, anus. The numbers of tubercles dorsally and ventrally on each annulus are indicated in the squares. Where mid-lateral tubercles are present this is indicated by a small arrow pointing downwards, to indicate that two of the tubercles counted as dorsal are actually mid-lateral. In this species numbers in brackets indicate small secondary tubercles which are situated para-marginally (terms such as this are illustrated in Fig. 11D). Numbers in a circle indicate the presence of small white tubercles which are in the intermediate line of the dorsal and ventral region of the annulus and usually visible laterally. There are no median tubercles in normal annuli. The size range 1–3, 3 being the largest, indicates the relative size of the annulus (and tubercles) compared with the annulus next to it. It does not attempt to indicate sizes of annuli from different parts of the body, since there is a decrease in annular size towards the body's extremities.

in the characters of the suckers, such as papillae and eyes, which appear to be fairly constant in other species. It is extremely doubtful whether either *P. moorei* or *P. bimaculata* is synonymous with *P. macrothela*.

On examining the type specimen of *Pontobdella afra* it was found to be the same as *Stibarobdella macrothela*. According to Baird (1869) tubercles are absent from the a_1 and a_3 annuli of the preclitellar region, and the clitellar region, but in fact they are present though much reduced in size.

Ringuelet (1944) made *Pontobdella papillata* Grube (1871) synonymous with *Stibarobdella macrothela*. *Stibarobdella superba* Leigh-Sharpe (1925), which was the type by monotypy of *Stibarobdella* Leigh-Sharpe, also appears to by synonymous with the latter so this older generic name is used in place of *Pontobdellina* Harding (1927). The earlier generic diagnosis seems, incidentally, to be more useful. On examining the type specimen of *Stibarobdella superba*, which is in a rather poor condition, it was found that the median papilla on the anterior sucker figured by Leigh-Sharpe was absent. Some of the primary tubercles on the dorsal surface bore sensillae arranged diagonally and the lateral tubercles on the a_1 and a_3 annuli often bore three small sensillae arranged longitudinally. However, since sensillae are highly variable and in some specimens apparently absent, there seem to be no grounds for separating this from *Stibarobdella macrothela*.

Richardson (1950), in his description of *Pontobdella benhami*, regarded the number of tubercles on the a_2 annulus of the testicular and caecal region as different in his leech and *Pontobdella macrothela*, i.e. eight and twelve respectively. Actually *S. macrothela* has eight primary tubercles, with an additional mid-ventral pair of medium size, making a possible ten primary tubercles. In addition to these there are secondary tubercles situated latero-dorsally and latero-ventrally, which are often obscured by the larger tubercles on each side. These small latero-dorsal tubercles were mentioned by Ringuelet (1944), Goddard (1909), Harding (1924) and Cordero (1937–38), but those lying latero-ventrally were not mentioned. The tuberculation agrees well with Richardson's description, which states that the a_2 annulus, in addition to the eight primary tubercles, may possess small tubercles without sensillae which may show clearly only on gorged specimens, and that a pair of mid-ventral secondary tubercles occur near the anterior border of the a_2 annulus. So the information available suggests that *Pontobdella benhami* is a synonym of *Stibarobdella macrothela*.

Goddard (1909) described a specimen of *Pontobdella macrothela*, found in Australia, which lacked any external markings and was possibly a preserved specimen which may have lost the ocular pigment patches on the anterior sucker. Cordero (1937–38) stated that *Pontobdella macrothela* may or may not possess tentacular papillae and pigmented ocular patches, but this variation seems unlikely within a single species. It may be noted that the dimensions of the suckers varied greatly amongst the forms grouped by Cordero, which suggests that different species were involved.

DISTRIBUTION. Widely distributed since it is found on numerous species of sharks. Specimens examined were from Gambia, Queensland, Japan, China, Barrier Reef Australia, Freemantle, British Guinana, Malindi (Kenya) and Coiba Island (Pacific).

They have also been recorded from Tandjong, Sumatra, Jamaica, New South Wales and the Bay of Bengal.

HOSTS. Black-tipped shark, *Carcharinus melanopterus* ; Tiger shark, *Galeocerdo arcticus* ; Hammer-head shark, *Sphyrna* sp. (Moore, 1927) ; *Eulamia* sp. ; *Scoliodon* sp. Found attached to fins, mouth and claspers.

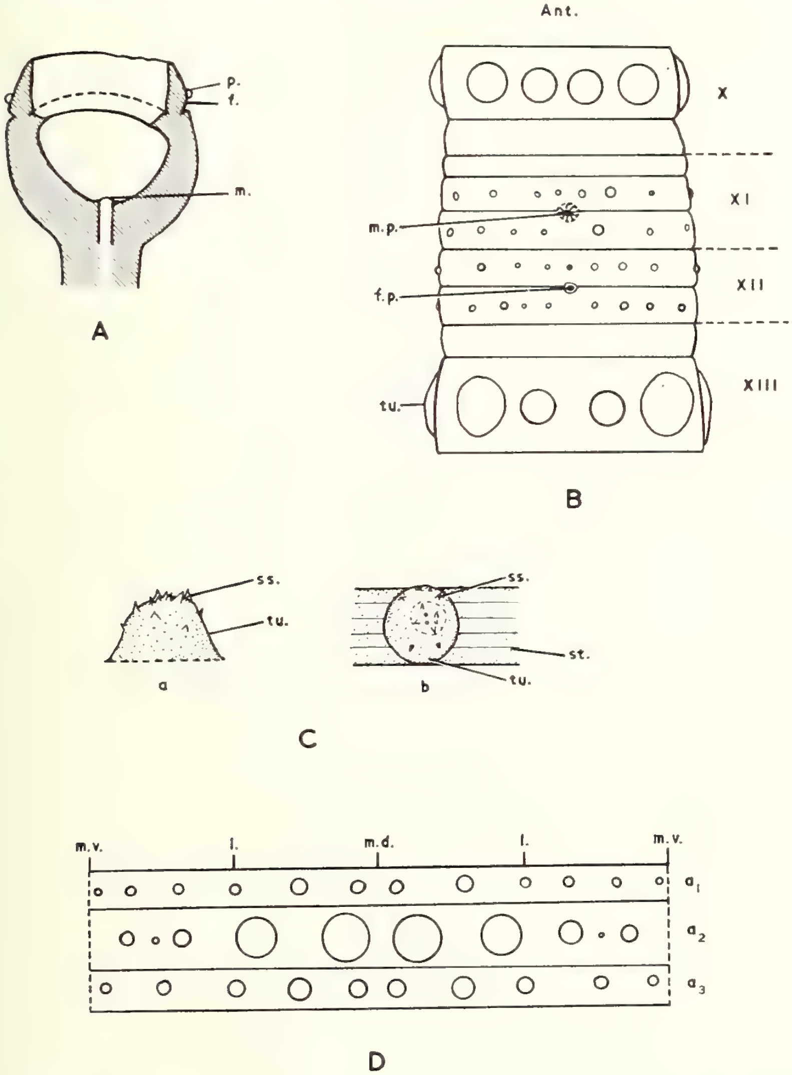


FIG. 14. *Stibarobdella loricata*. A. Section through anterior sucker, showing oral surface. B. Ventral surface of clitellar constriction, showing position of genital pores and tubercles. C. (*a*) Tubercle with sensillae. (*b*) Tubercle on annulus showing striae. D. Tuberculation of a typical triannulate somite split mid-ventrally. *f.*, fringe ; *st.*, stria ; *tu.*, tubercle. See Fig. 11 (p. 406) for other abbreviations.

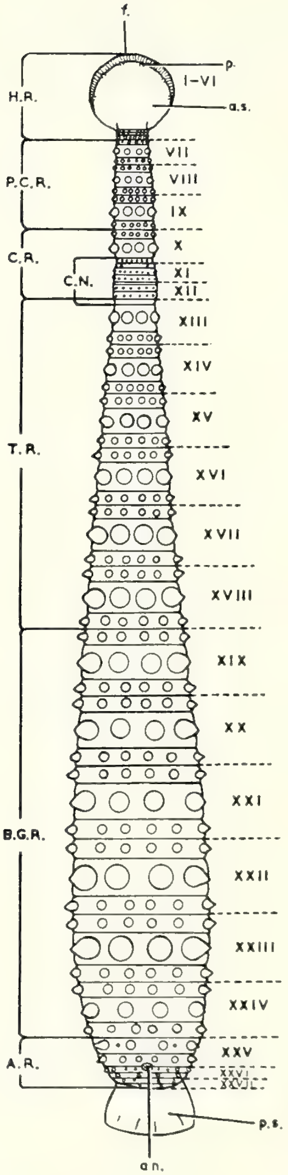

f.
p.
I–VI
H.R.
a.s.
VII
VIII
P.C.R.
IX
X
C.R.
XI
C.N.
XII
XIII
XIV
XV
T.R.
XVI
XVII
XVIII
XIX
XX
XXI
B.G.R.
XXII
XXIII
XXIV
XXV
A.R.
XXVI
XXVII
p.s.
an.

FIG. 15. Dorsal view of *Stibarobdella loricata* showing annulation, tuberculation and suckers. *f.*, fringe. See Fig. 12 (p. 407) for other abbreviations.

Stibarobdella loricata (Harding, 1924)

Pontobdella loricata Harding, 1924 : 39.
Stibarobdella loricata : Harant, 1929 : 651.

DESCRIPTION. *General Characters.* About a dozen specimens were examined. The body is fusiform, tapering gradually towards the anterior end, up to 16·6 cm. long and circular in cross-section when fully gorged, but somewhat flattened dorsoventrally in starved specimens.

Although presumably faded, due to preservation in alcohol, and without external markings, the colour varied between pale yellow, green and brown. The anterior sucker is cup-shaped and attached eccentrically so that the dorsal surface is longer than the ventral. It is generally circular but may be slightly flattened laterally, so that its opening becomes slit-like. It possesses a marginal fringe and generally three pairs of inconspicuous papillae on each side (Text-figs. 14A and 15). The anterior sucker is often about equal in size to the posterior sucker, but when both are fully expanded the latter is slightly larger. The anterior sucker is usually three times the diameter of its point of attachment but never exceeds the greatest diameter of the body. The posterior sucker is cup-shaped when contracted and its diameter is then less than the greatest diameter of the body, but when expanded it is approximately equal to it. It is attached centrally and is greater in diameter than its point of attachment.

ANNULATION. Uniannulate somites } XXVII. (Text-fig. 15)
Biannulate somites XXV ; XXVI } } XII.
Triannulate somites VII–XI ; XIII–XVXI }

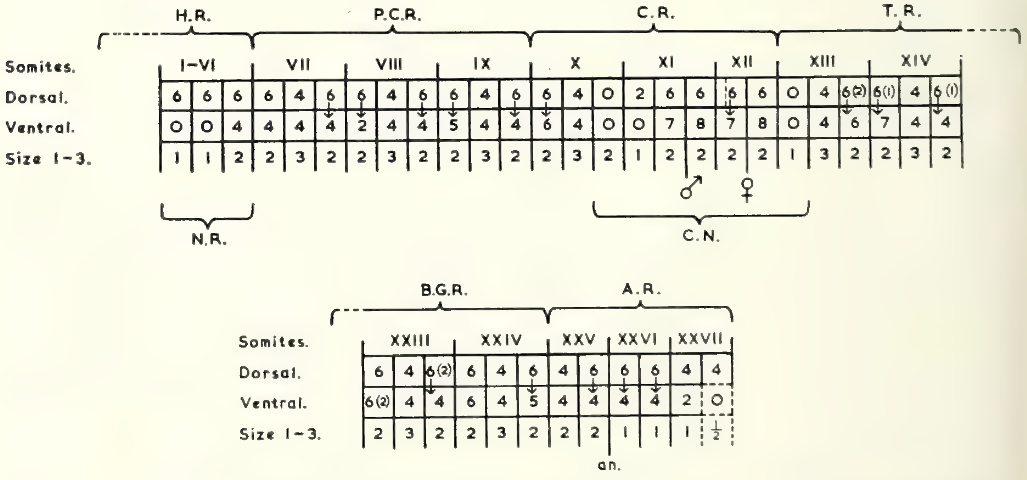
The first three annuli, the anterior two of which are smallest, constitute the neck. The three preclitellar somites, VII–IX, are all trimeric, with the annular and tubercular sizes of each somite in the ratio 1 : 2 : 1.

All eight annuli of the clitellar constriction, i.e. Xa_3 to $XIIIa_1$ inclusive, are greatly reduced and approximately equal in size (Text-figs. 14B and 15). Somite XI always appears to be triannulate and includes the male pore, which is situated mid-ventrally in the furrow between a_2 and a_3. Somite XII is clearly divided dorsally into three annuli, but the anterior annulus is small, non-tuberculate and indistinguishable ventrally, where the female pore lies between a_2 and a_3. The testicular somite XIII–XVIII are all trimeric, with annular widths and tubercular sizes in the ratio 1 : 2 : 1. The somites of the caecal region XIX–XXIV are similar, and the body is generally broadest at about somite XXII. The annulation of the three anal somites XXV–XXVII varies considerably, with annular widths decreasing towards the posterior end. Somites XXV and XXVI are biannulate and reduced ventrally. Somite XXVII may be uniannulate or biannulate. If the latter, the last annulus of the somite is generally unrecognizable ventrally. The anus is situated dorsally in the furrow between somite XXV and XXVI. Annulation and tuberculation vary towards the extremities of the body, where there is some ventral curvature.

TUBERCULATION (Text-fig. 16). Harding (1924 and 1927) gave the normal number of tubercles on a_1 and a_3 as fourteen, six dorsal, six ventral and a pair lateral, but in my specimens the more usual number was twelve, six dorsal and six ventral, with lateral tubercles occurring rather irregularly. The number varied from ten to fourteen, a_3 tending to have fewer than a_1.

The first two annuli of the neck region were extremely small and tubercles were never obvious on their ventral surfaces. In one specimen there were only five tubercles, instead of the normal six, on the dorsal surfaces of a_1 and a_3 annuli in the preclitellar region. The tuberculation of the clitellar constriction varied considerably and the tubercles were small and irregularly placed. Xa_3, XIa_1 and $XIIIa_1$ were often free of tubercles, but occasionally XIa_1 bore a minute pair dorsally. Most of the remaining annuli of the clitellar constriction bore between twelve and fourteen tubercles per annulus. Tuberculation of a typical trimeric somite is shown in Text-fig. 14D, the larger tubercles being dorsal in position. Small tubercles were present dorsally on the last annulus of somite XXVII, which is generally indistinguishable ventrally.

In many of the specimens each annulus possessed between four and seven striae dividing it up into smaller rings (Text-fig. 14C), but these were variable and absent in some specimens, particularly the smaller ones. Selensky (1915), in discussing the annulation of some Pontobdellinae, stated that the somite is divided into fourteen or fifteen secondary annuli. Out of the six species which I have examined, including nearly one hundred specimens, *Stibarobdella loricata* is the only species showing such subdivisions. Moreover, their presence depends on whether the specimen is gorged or starved, whereas true annuli are more permanent. Minute tubercles are never found on these small rings and a large tubercle may cover four or five of them. The



Somites.	I–VI			VII			VIII			IX			X			XI			XII		XIII			XIV		
Dorsal.	6	6	6	6	4	6↓	6↓	4	6↓	6↓	4	6↓	6↓	4	0	2	6	6	6↓	6	0	4	6(2)↓	6(1)↓	4	6(1)↓
Ventral.	0	0	4	4	4	4	2	4	4	5	4	4	6	4	0	0	7	8	7	8	0	4	6	7	4	4
Size 1–3.	1	1	2	2	3	2	2	3	2	2	3	2	2	3	2	1	2	2	2	2	1	3	2	2	3	2

Somites.	XXIII			XXIV			XXV		XXVI		XXVII	
Dorsal.	6	4	6(2)↓	6	4	6↓	4	6↓	6↓	6↓	4	4
Ventral.	6(2)	4	4	6	4	5	4	4	4	4	2	0
Size 1–3.	2	3	2	2	3	2	2	2	1	1	1	½

FIG. 16. Diagram illustrating the tuberculation of a single specimen of *Stibarobdella loricata*, anterior extremity above, posterior below. The numbers in brackets in this diagram indicate the presence of small secondary tubercles which are generally situated paramarginally. " ½ " in the size column indicates the presence of an annulus dorsally only See Fig. 13 (p. 409) for other abbreviations.

tubercles (Text-fig. 14C*a* and *b*) are generally quite prominent and bear sensillae, which are usually concentrated at the summits but may be present over the whole tubercle.

DISTRIBUTION. Off Cabinda, West Coast of Central Africa ; West Coast of Mexico and Peru ; India ; Sierra Leone and Philippine Islands.

HOSTS. Unrecorded but the wide distribution suggests oceanic sharks.

Stibarobdella bimaculata (Oka, 1910)

Pontobdella bimaculata Oka, 1910 : 171.

DESCRIPTION. *General characters.* One specimen examined. This species is very close to *Stibarobdella tasmanica* (p. 420), but may provisionally be regarded as separate. Only one specimen was found in the British Museum collection and this resembled Oka's (1910 and 1927) description very closely. Harant (1929) seems to be wrong in assuming this to be a quadriannulate form. In this specimen the body is elongated, distended, flattened and brown, but in Oka's it was cylindrical and yellow. The specimen was 3 cm. long and 5 mm. wide.

The anterior sucker (Text-figs. 17A and 18) is circular, attached eccentrically, and separated from the body by a neck. The diameter of this sucker in the contracted state is slightly broader than the preclitellar region, but according to Oka it may be nearly twice as broad when expanded. It carries three pairs of marginal elongated papillae, a smaller pair situated near the base of the sucker, and a pair of large rectangular eye patches of a dark reddish brown colour. A few concentric grooves can be seen at the base of the sucker. The posterior sucker is bell-shaped, scarcely larger than the anterior sucker and separated from the body by a constriction.

ANNULATION. Uniannulate somites XXVII (Text-fig. 18)
Biannulate somites XXV, XXVI } XI, XII, (VII?).
Triannulate somites VIII–X, XIII–XXIV }

The posterior limit of the neck is doubtful in this species, since Oka (1927) called the third and fourth annulus a double annulus because they were usually poorly separated. But it seems doubtful whether both these two annuli should be regarded as lying in the neck region, making a total of four annuli there, for that would involve regarding the first preclitellar somite VII as biannulate, with the anterior annulus the largest, whereas it is triannulate in other *Stibarobdella*. The other two preclitellar somites VIII and IX are triannulate with their annular widths 1 : 2 : 1.

Of the annuli in the clitellar constriction, Xa$_3$ is very small. Somites XI and XII may be regarded as biannulate, with the anterior annulus double, forming a smaller anterior ring, which can scarcely be regarded as a separate annulus. The male pore is situated mid-ventrally in the furrow between the two major annuli of somite XI, while the female pore is similarly situated in somite XII. Annulus XIIIa$_1$ is very small. Somites XIV to XXIV are all triannulate, with annular widths in the ratio 2 : 3 : 2. The outline of the nerve chain could be made out on the ventral surface, with the ganglia on the a$_2$ annulus of each somite. Somites XXV and XXVI are biannulate, with the anus situated dorsally on the a_1 annulus of somite XXVI. Somite XXVII is very small and indistinguishable ventrally, but according to Oka (1927) may be double.

TUBERCULATION (Text-fig. 19). In the clitellar constriction, annuli Xa_3 and $XIIIa_1$ possess no tubercles and all the other tubercles of this region are small. The tuberculation on somites VIII, IX and XIV–XXIV is fairly constant (see also Text-fig. 17C). The a_2 annulus of a typical somite has four large dorsal tubercles and four smaller ventral ones, and the a_1 and a_3 annuli generally have six dorsal and four slightly smaller ventral ones. The tubercles are conical, generally with between six and ten apical sensillae.

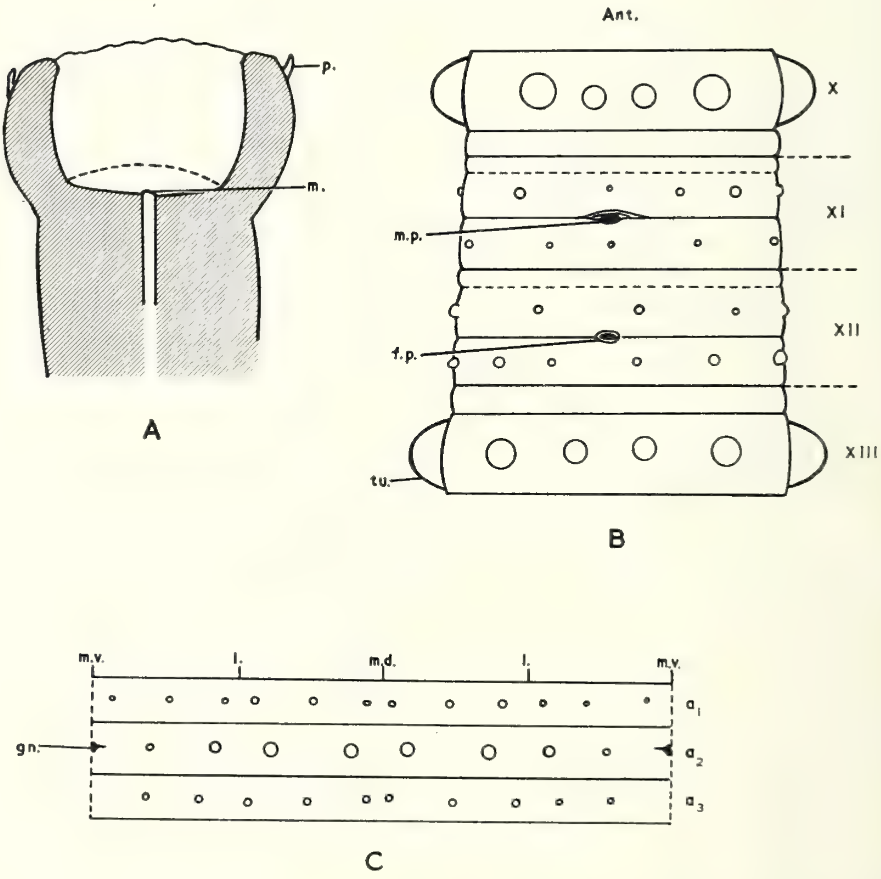


FIG. 17. *Stibarobdella bimaculata*. A. Section through anterior sucker, showing oral surface. B. Ventral surface of clitellar constriction, showing position of genital pores and tubercles. C. Tuberculation of a typical triannulate somite split mid-ventrally. *gn.*, outline of ganglion on ventral surface; *tu.*, tubercle; See Fig. 11 (p. 406) for other abbreviations.

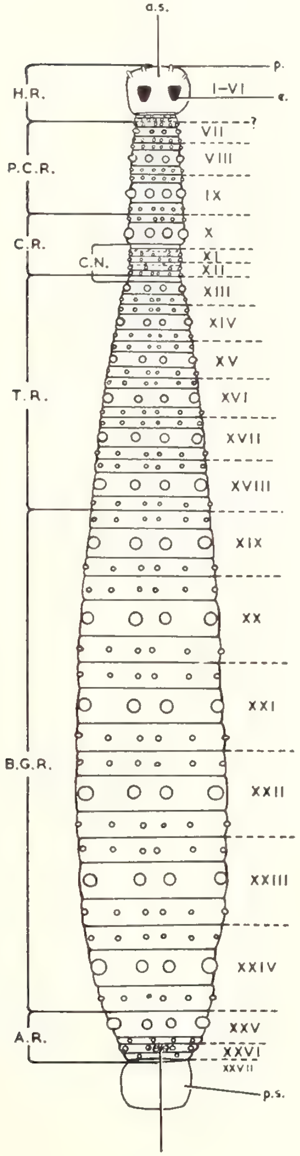

a.s.
p.
H.R.
I–VI
e.
?
VII
P.C.R.
VIII
IX
C.R.
X
C.N.
XI
XII
XIII
XIV
XV
T.R.
XVI
XVII
XVIII
XIX
XX
XXI
B.G.R.
XXII
XXIII
XXIV
A.R.
XXV
XXVI
XXVII
p.s.
an.

FIG. 18. Dorsal view of *Stibarobdella bimaculata* showing annulation, tuberculation and suckers. See Fig. 12 (p. 407) for abbreviations.

REMARKS. Both *Stibarobdella bimaculata* and *S. moorei* (p. 422) differ from *S. macrothela* in having the posterior sucker only slightly wider than the anterior sucker and only eight tubercles on the a_2 annulus. Their tubercles are also very different in appearance. They should not be regarded as synonymous as suggested by Cordero (1937–38).

DISTRIBUTION. Pearl Island, Panama ; Hondo (Coast of Sagami Awa).

HOST. Sharks.

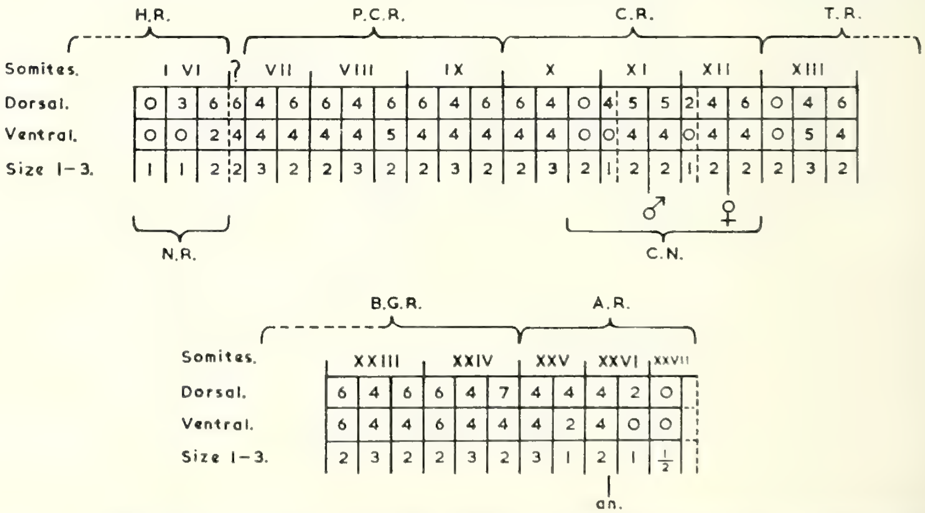
Stibarobdella planodiscus (Baird, 1869)

Pontobdella planodiscus Baird, 1869 : 312.
Pontobdella variegata Baird, 1869 : 313.

DESCRIPTION. *General characters.* Three specimens were examined, 40–55 mm. in length and 5–7 mm. in breadth. The body is elongated, yellowish and cylindrical or flattened. Baird (1869) named the cylindrical specimens *Pontobdella variegata*, but in fact they seem to be the same species as the flattened one, which he described as *P. planodiscus* and which has page priority.

The anterior sucker (Text-fig. 20A) is circular and attached eccentrically with its dorsal surface elongated. It is less than twice as broad as the neck at its narrowest point. It bears four pairs of papillae, of which the ventral pair are very small and often difficult to see, and no marginal fringe.

The posterior sucker when contracted is equal in width to its point of attachment and separated from the body only by a shallow groove, but when expanded is half



Somites.	I VI		?	VII			VIII			IX			X			XI			XII			XIII	
Dorsal.	O	3	6	6	4	6	6	4	6	6	4	6	6	4	O	4	5	5	2	4	6	O	4	6
Ventral.	O	O	2	4	4	4	4	4	5	4	4	4	4	4	O	O	4	4	O	4	4	O	5	4
Size 1–3.	1	1	2	2	3	2	2	3	2	2	3	2	2	3	2	1	2	2	1	2	2	2	3	2

Somites.	XXIII			XXIV			XXV		XXVI		XXVII
Dorsal.	6	4	6	6	4	7	4	4	4	2	O
Ventral.	6	4	4	6	4	4	4	2	4	O	O
Size 1–3.	2	3	2	2	3	2	3	1	2	1	$\frac{1}{2}$

FIG. 19. Diagram illustrating the tuberculation of a single specimen of *Stibarobdella bimaculata*, anterior extremity above, posterior below. ? indicates where the limits of the somites are uncertain. " $\frac{1}{2}$ " in the size column indicates the presence of an annulus dorsally only. See Fig. 13 (p. 409) for other abbreviations.

as broad again (Text-fig. 20B). The anterior : posterior sucker ratio when contracted is 1 : 1 : 6.

ANNULATION. Uniannulate somites XXVI, XXVII.
Biannulate somites XI, XII, XXV.
Triannulate somites VII–X, XIII–XXIV.

The three preclitellar somites VII–IX are triannulate, with annular widths in the ratio 2 : 3 : 2. The clitellar constriction (Text-fig. 20C) is made up of small annuli with somites XI and XII biannulate. The male and female pores lie in the grooves between the two annuli of somites XI and XII respectively. Somites XIV to XXIV are all triannulate, with their annular widths in the ratio 2 : 3 : 2. The first anal somite XXV is biannulate, with the anus situated mid-dorsally on the first annulus. Somites XXVI and XXVII consist of single small annuli which are reduced further ventrally.

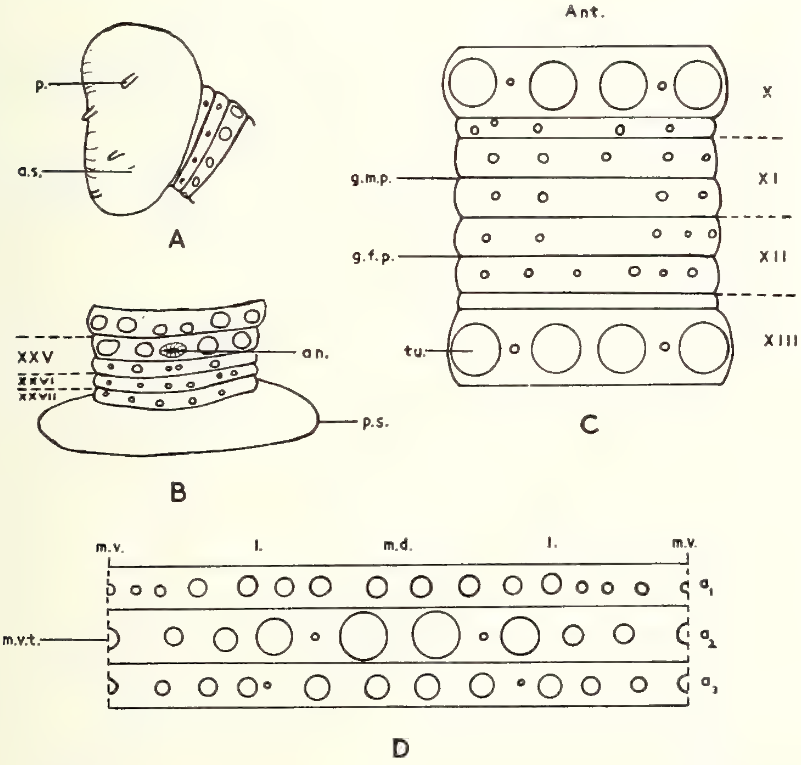


FIG. 20. *Stibarobdella planodiscus*. A. Anterior sucker. B. Posterior sucker. C. Dorsal surface of clitellar region. D. Tuberculation of a typical triannulate somite split mid-ventrally. *an.*, anus; *a.s.*, anterior sucker; *g.f.p.*, groove in which female pore is situated; *g.m.p.*, groove in which male pore is situated; *m.v.t.*, mid-ventral tubercle; *p.s.*, posterior sucker; *tu.*, tubercle. See Fig. 11 (p. 406) for other abbreviations.

Tuberculation. The normal triannulate somite (Text-fig. 20D) has nine tubercles on the a_2 annulus, four large tubercles situated dorsally and five smaller ventrally, of which one is mid-ventral. The a_1 annulus possesses between fourteen and sixteen tubercles and the a_3 annulus generally eleven. The ventral tubercles in both cases are smallest. Tubercles on annuli in the clitellar constriction are much smaller, more irregular in number and absent from the $XIIIa_1$ annulus. Tubercles are also small and irregular on the last three annuli of the anal region and are often indistinguishable on the ventral side of the annulus of somite XXVII. The tubercles are mammiform, with sensillae at their summit.

Remarks. It appears that the two species described by Baird (1869) as *Pontobdella variegata* and *Pontobdella planodiscus* are the same. According to Baird the major differences were that *P. planodiscus* had a flattened body, apical sensillae on the tubercles and three pairs of papillae on the anterior sucker, while *P. variegata* had a cylindrical body, rounded tubercles and no papillae. However, examination of his material, including the cotypes, showed that the flattening of *P. planodiscus* was similar to that seen as a preservation artefact in other species and that the anterior sucker had three pairs of large papillae and one pair of small ones. Three pairs of retracted papillae were also discernible on *P. variegata*. Since the presence of sensillae at the summit of tubercles is also highly variable, there seems from the material available to be no reason for regarding these as separate species.

The sucker characters and mid-ventral tubercles of *Stibarobdella planodiscus* are similar to those of the quadriannulate form *Pontobdella vosmaeri*, indicating parallel evolution.

Distribution. Straits of Magellan ; Possession Bay, Patagonia.

Host. Not recorded.

Stibarobdella tasmanica (Hickman, 1946)

Pontobdella tasmanica Hickman, 1946 : 27, nom. nov. pro *Pontobdella verrucosa* Hickman, 1941 : 41 (non *Hirudo verrucosa* Fleming, 1811 : 245).

Description. *General characters.* (Specimens not examined. Apparently originally described from a single specimen, although Ingram (1957) described further specimens.) Body 37 mm. long, fusiform, circular in section and narrowing anteriorly. Colour light brown, becoming mustard yellow on preservation. Single dark brown triangular patch on the dorsal side of the anterior sucker. Large tubercles tipped with white and apparently mammiform. Anterior sucker 2·26 mm. in diameter, cup-shaped, eccentrically attached and with four pairs of submarginal papillae and twelve radial furrows on its oral surface. No eyes. Posterior sucker cup-shaped, 3·54 mm. in diameter, centrally attached and slightly wider than the greatest width of the body. Anterior : posterior sucker ratio between 1 : 1 and 1 : 2

Annulation. Uniannulate somites XXVII ⎫ XXV, XXVI. (Somites numbered
Biannulate somites X–XII ⎭ as in *S. macrothela*.
Triannulate somites VII–IX, XIII–XXIV. Text-fig. 12.)

Somites of the testicular and caecal regions have annular widths in the ratio 2 : 3 : 2. Clitellar constriction between a_2 annuli of somites X and XIII, consisting of five narrow rings. Male pore originally described as lying in furrow between somite XI and XII, but according to Ingram (1957) opening between XIa_2 and a_3, suggesting that this somite is triannulate. Female pore in furrow between somite XII and XIII. Somite XXV divided into two annuli only ventrally and somite XXVI divided into two only dorsally. Anus near posterior edge of annulus $XXVIa_1$.

TUBERCULATION. A_2 annuli each possess four large dorsal tubercles and four smaller ventral ones. A_1 and a_3 annuli have six dorsal and six ventral tubercles with the two dorso-median tubercles smallest, and a ventro-median tubercle often present. Interposed tubercles common.

DISTRIBUTION. Sandy Bay, Hobart ; Kingston, Jamaica ; Brig Rocks, King Island.

HOST. Skate (Ingram, 1957).

Stibarobdella taprobanensis (de Silva, 1963)

Pontobdella taprobanensis de Silva, 1963*b* : 39.

DESCRIPTION. *General characters.* (Specimens not examined.) Body up to 29 mm. long (including suckers). Preclitellar region translucent (enabling underlying organs to be seen). Rest of body yellowish brown, with pairs of brown spots dorsally on testicular and caecal region. Anterior sucker deeply cupped and slightly wider than preclitellar region, with dorsal margin three times the length of ventral margin, incised, shovel shaped, and bearing dorsally a pair of vermilion coloured blotches which meet anteriorly and two pairs of eyes, but no papillae. Anterior : posterior sucker ratio between 1 : 1·3 and 1 : 2. Posterior sucker with dark radial bands and a smooth margin, oval, sometimes folded dorso-ventrally, eccentrically attached, so that the dorsal portion is twice the ventral portion, and equal to or less than the maximum diameter of the body.

ANNULATION AND TUBERCULATION. Uniannulate somites (XXV–XXVII)?
Biannulate somites XI, XII.
Triannulate somites VII–X, XIII–XXIV.
(Somites numbered as in *S. macrothela*, Text-fig. 12.)

No true tubercles, but only slightly protuberant opaque patches, segmentally arranged. Two small neck annuli. Preclitellar annuli VII–X triannulate, a_2 annuli largest and possessing two opaque patches dorso-laterally and two ventro-laterally, composed of groups of small opaque spots, which are distributed sparsely elsewhere. Annuli a_1 and a_3 possess a pair of opaque patches dorsally only. Preclitellar constriction in usual position, between Xa_3 and $XIIIa_1$. Somite XI and XII without opaque patches. Male pore mid-ventral, in the middle of somite XI. Female pore mid-ventral, in middle third of somite XII. A_2 annuli of somites XIII–XXIV with two pairs of opaque patches (rosettes) dorsally, situated para-marginally and para-medially, and composed of two to six triangular opaque areas. Mid-dorsal ellipsoidal umber coloured clear areas on all annuli. No rosettes ventrally or on somites posterior to somite XXIV. Anus mid-dorsal between somites XXVI and XXVII.

Distribution. Wadge Bank, Ceylon.

Host. Unknown.

Stibarobdella moorei (Oka, 1910)

Pontobdella moorei Oka, 1910 : 171.
Stibarobdella moorei : Harant, 1929 : 651.

Description. *General characters.* (Specimens not examined.) Body up to 14 cm. long and 14 mm. broad, fusiform, yellowish and thickest in the middle of the posterior half. Anterior sucker smooth, hemispherical, rather large, and without fringe, eyes, papillae or annular marks. Posterior sucker bell-shaped, scarcely larger than anterior sucker and separated from the body by a constriction.

Annulation. Uniannulate somites—none.
Biannulate somites XI, XII, XXV–XXVII. (Somite numbering as
Triannulate somites VII–X, XIII–XXIV. in *S. macrothela*,
Text-fig. 12.)

Triannulate somites have annular widths in the ratio 3 : 4 : 3. Neck of three annuli, the posterior largest and the anterior two often hidden by sucker. Preclitellar region of three triannulate somites. Clitellar constriction as usual between a_2 annuli of somites X and XIII. Somites XI and XII biannulate and bearing between their annuli the male and female pores respectively. Somites XXV–XXVII biannulate, becoming smaller posteriorly. Anus on a_1 or between a_1 and a_2 of somite XXVI.

Tuberculation. A_2 annuli with four prominent tubercles dorsally and four ventrally, each bearing 7–10 apical sensillae. A_1 and a_3 annuli with ten smaller tubercles, four dorsally, four ventrally and two laterally. Tubercles on clitellar constriction are smaller still and absent from annulus Xa_3 and sometimes from $XIIIa_1$.

Distribution. Hondo (Coast of Sagami, Awa). Coast of Tokyo.

Host. Shark.

Stibarobdella australiensis (Goddard, 1909)

Pontobdella australiensis Goddard, 1909 : 724.

Description. *General characters.* (Specimens not examined.) Body up to 20 mm. long and 3 mm. broad, attenuated anteriorly and circular in cross-section, extremities yellowish brown, the rest bluish grey. Anterior sucker 1 mm. in diameter, with four or five pairs of papillae (the posterior pair inconspicuous or absent), two faint annuli on dorsal surface and no fringe or pigmented markings. Posterior sucker 1·5 mm. in diameter, with five or six annuli on dorsal surface. Anterior : posterior sucker ratio 1 : 1·5.

Annulation. Uniannulate somites }
Biannulate somites XI, XXV, XXVI } XXII, XXVII
(Somite numbering as for *S. macrothela*, Text-fig. 12.)
Triannulate somites VII–X, XIII–XXIV

In triannulate somites a_2 is slightly larger than annuli a_1 and a_3 and possesses more prominent tubercles.

Tuberculation. Tubercles largest in the testicular and caecal regions, where the a_2 annuli each bear six prominent conical papillae, four dorsal, situated para-medially and para-marginally, and two ventral, situated para-marginally. These ventral tubercles are smaller and similar in size to tubercles of a_1 and a_3 annuli. Dorsal tubercles are larger than a_1 and a_3 tubercles.

Distribution. Not recorded.

Host. Not recorded.

Genus ***PONTOBDELLA*** Leach, 1815

Pontobdella Leach, 1815 : 9.

Type species. *Hirudo muricata* Linnaeus.

Diagnosis. Somites of the testicular and caecal regions tetrameric.

Pontobdella muricata (Linnaeus, 1758)

Hirudo muricata Linnaeus, 1758 : 650.
Hirudo verrucosa Fleming, 1811 : 245.
Pontobdella verrucata Leach, 1815 : 11.
Pontobdella areolata Leach, 1815 : 10.
Pontobdella spinulosa Leach, 1815 : 12.
Pontobdella muricata : de Blainville, 1818 : 293 ; Harding, 1910 : 143.
Pontobdella laevis de Blainville, 1827 : 243.
Pontobdella verrucosa : Leydig, 1851 : 318.

Description. *General characters.* (About fifty specimens examined.) The body is club-shaped, generally circular in cross-section or slightly flattened dorso-ventrally in some starved specimens, and up to 19·0 cm. long (excluding suckers). The colour varies from dull yellow to olive green or occasionally pinkish.

The cup-shaped anterior sucker (Text-fig. 21A and 22) is between two and three times the diameter of the neck and is generally as large as or larger than the posterior sucker. It is circular and fixed eccentrically, so that the dorsal surface is longer than the ventral. Around its edge is a very noticeable fringe, bearing three pairs of lateral papillae, which are sometimes retracted and obscure. The sucker may be somewhat flattened laterally and then appears to have a slit-like opening.

The posterior sucker is cup-shaped when contracted, centrally fixed and generally just broader than its point of attachment, although considerably larger when expanded. It never exceeds the maximum diameter of the body.

ANNULATION. Uniannulate somites —
Biannulate somites XI, XII, XXV, XXVI, XXVII.
Triannulate somites VII–X. Text-fig. 22.
Quadriannulate somites XIII–XXIV.

The first three annuli constitute the neck and the anterior two of these are much smaller than the other. The three preclitellar somites VII–IX are all triannulate with their annular and tubercular sizes in the ratio 1 : 2 : 1. The clitellar constriction includes the small annuli Xa_3 and $XIIIa_1$, between which are from four to six annuli,

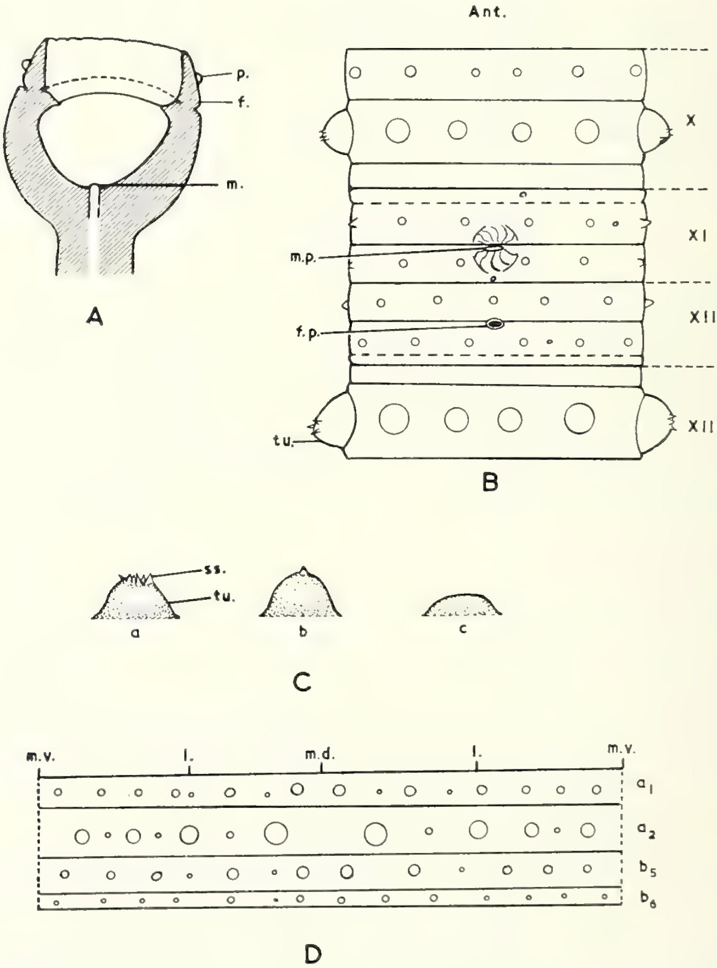


FIG. 21. *Pontobdella muricata.* A. Section through anterior sucker, showing oral surface. B. Ventral surface of clitellar constriction, showing position of genital pores and tubercles. C. a, b and c: Tubercles in various stages of contraction. D. Tuberculation of a typical quadriannulate somite split mid-ventrally. For designation of annuli, i.e. a_1, a_2, b_5 and b_6, see Mann 1953; *f.*, fringe; *tu.*, tubercles; See Fig. 11 (p. 406) for other abbreviations.

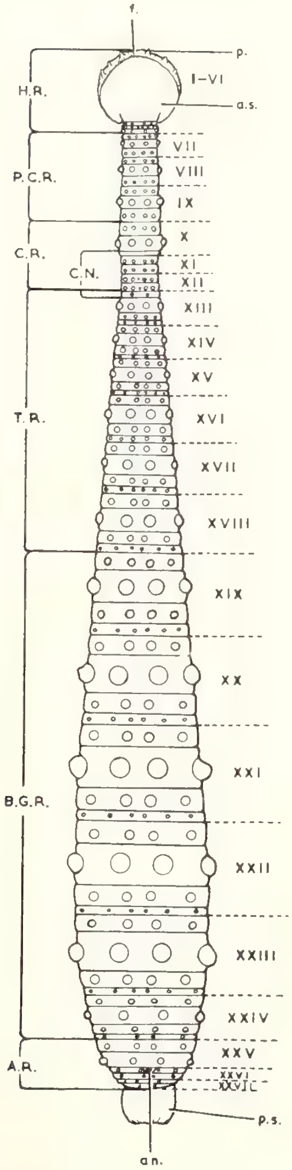

f.
p.
I–VI
a.s.
H.R.
VII
VIII
P.C.R.
IX
X
C.R.
C.N.
XI
XII
XIII
XIV
XV
T.R.
XVI
XVII
XVIII
XIX
XX
XXI
B.G.R.
XXII
XXIII
XXIV
XXV
A.R.
XXVI
XXVII
p.s.
an.

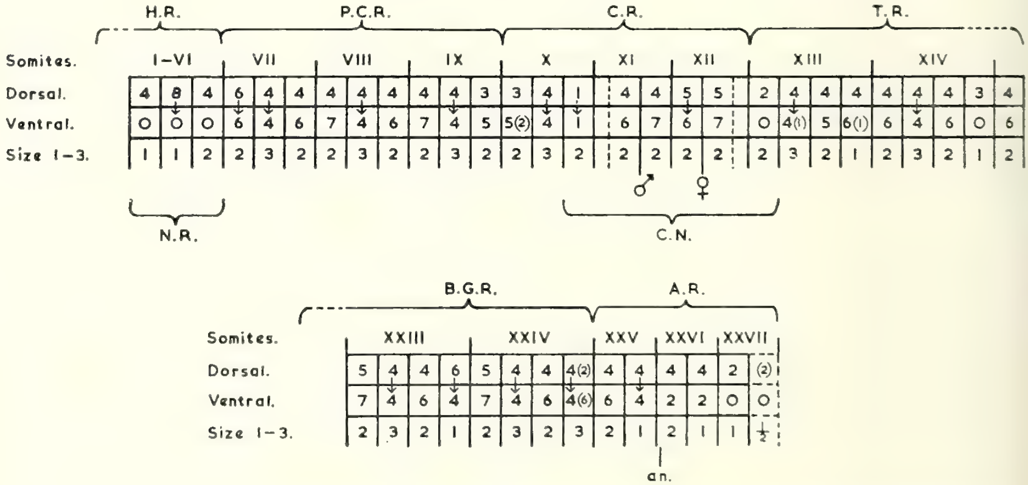
FIG. 22. Dorsal view of *Pontobdella muricata* showing annulation, tuberculation and suckers. *f.*, fringe ; See Fig. 12 (p. 407) for other abbreviations.

two or three per somite (see dotted lines in Fig. 21D). The appearance of these extra subdivisions may depend on the stage of gorging or contraction of the specimen. The male pore is situated in the furrow between a_1 and a_2, or a_2 and a_3 of somites XI (depending upon whether this somite is bi- or triannulate), while the female pore is situated between a_1 and a_2 of somite XII. Somites XIII to XXIV are all quadriannulate and their annular widths and tubercular sizes vary in the ratio of 2 : (3 or 4) : 2 : 1.

The annulation of the three anal somites XXV–XXVII is rather indistinct, but it appears that there are two annuli per somite, decreasing in size posteriorly. The last two small annuli are often unrecognizable and nearly always absent from the ventral surface. The anus is mid-dorsal in somite XXVI, either between the two annuli, or in the middle of the anterior annulus.

TUBERCULATION. Text-fig. 23 shows the arrangement of tubercles towards the anterior and posterior extremities of the body. Text-fig. 21D shows the tuberculation of a typical quadriannulate somite. Dorsal tubercles tend to be larger than ventral ones. The a_2 annulus has eight primary tubercles, between which may lie 0–6 secondary tubercles. The a_1 annulus has generally about twelve primary tubercles and up to six secondary tubercles. The b_5 annulus has about ten primary tubercles and up to six secondary tubercles, and the b_6 annulus about fourteen small tubercles.

The tubercles on the first two small annuli of the neck region are much reduced and often absent from the ventral surface. In the clitellar constriction the tubercles are much reduced and irregular in arrangement. Annuli Xa_3 and $XIIIa_1$ often have



Somites.	I–VI			VII			VIII			IX			X			XI		XII		XIII				XIV				
Dorsal.	4	8 ↓	4	6 ↓	4 ↓	4	4	4 ↓	4	4	4 ↓	3	3	4 ↓	1 ↓	4	4	5 ↓	5	2	4 ↓	4	4	4	4 ↓	4	3	4
Ventral.	0	0	0	6	4	6	7	4	6	7	4	5	5(2)	4	1	6	7	6	7	0	4(1)	5	6(1)	6	4	6	0	6
Size 1–3.	1	1	2	2	3	2	2	3	2	2	3	2	2	3	2	2	2	2	2	2	3	2	1	2	3	2	1	2

Somites.	XXIII				XXIV				XXV		XXVI		XXVII	
Dorsal.	5	4 ↓	4	6 ↓	5	4 ↓	4	4(2) ↓	4	4 ↓	4	4	2	(2)
Ventral.	7	4	6	4	7	4	6	4(6)	6	4	2	2	0	0
Size 1–3.	2	3	2	1	2	3	2	3	2	1	2	1	1	½

FIG. 23. Diagram illustrating the tuberculation of a single specimen of *Pontobdella muricata*, anterior extremity above, posterior below. The numbers in brackets in this diagram indicate a regular increase in numbers of tubercles found in this region in other specimens. Secondary tubercles are not indicated here because of their irregularity. "½" in the size column indicates the presence of a small annulus dorsally only. See Fig. 13 (p. 409) for other abbreviations.

no tubercles, and when present these are more usually found dorsally. In the anal region too, tubercles are few or absent on the ventral surfaces of the annuli.

Remarks. Harding (1910) observed that the shape of the tubercles can vary considerably depending on whether the leech is relaxed, gorged or otherwise (Fig. 21C*a*, *b*, *c*). According to Selensky (1915), muscle fibres can pull down the tips of the tubercles, so that the skin becomes smooth. This has led to considerable confusion and the erection of numerous invalid species. *Pontobdella muricata* was described as having tubercles possessing a rosette of sensillae on their summit, *P. verrucata* as having mammiform tubercles without a rosette of sensillae, *P. areolata* as having tubercles forming low irregular prominences and *P. laevis* as having entirely retracted tubercles. It is possible, however, that *P. laevis* is not one of the Pontobdellinae (Moquin-Tandon, 1846).

Pontobdella verrucosa, according to Moquin-Tandon (1846) was distinguished by each quadriannulate somite having one large annulus and three small annuli, compared with three large annuli and one small in *P. muricata*. There are no grounds for the former species, since in fact *P. muricata* somites usually have one large annulus a_2, two medium sized annuli a_1 and b_5, and one small annulus b_6.

Distribution. Mediterranean Sea, North Sea and most waters in north-east Atlantic.

Hosts. Many species of rays and sometimes plaice.

Pontobdella vosmaeri Apathy, 1888.

Pontobdella vosmaeri Apathy, 1888 : 59.
Pontobdella brumpti Rivière, 1925 : 292.

Description. *General characters.* (Five specimens examined.) The body is club-shaped, circular in cross-section and may reach a length of 7·5 cm. (excluding suckers). The colour is dull yellow and usually uniform. The neck region is only slightly smaller than the diameter of the anterior sucker, the ratio in size being about 1 : 1·3. The anterior posterior sucker ratio is about 1 : 2. The anterior sucker (Text-fig. 24A and 25) is circular, cup-shaped and fixed eccentrically, so that the dorsal surface is somewhat larger than the ventral. The margin is without a fringe but generally bears three pairs of papillae. The posterior sucker is cup-shaped when contracted and fixed to the body centrally. It is generally slightly thicker than the body at its point of attachment, although when expanded it may be considerably larger, but never exceeding the maximum diameter of the body.

Annulation.	Uniannulate somites	XXVI, XXVII.		
	Biannulate somites	XI, XII, XXV	VII.	Text-fig. 25.
	Triannulate somites	VIII, X		
	Quadriannulate somites	XIII–XXIV	IX.	

The dorsal surface of the anterior sucker is sometimes faintly marked by three transverse furrows. The neck region includes the first three annuli, the anterior two of which are much smaller than the other. The annulation of the three preclitellar somites is quite different from *Pontobdella muricata.* Somite VII is generally biannulate, but occasionally there is a much reduced anterior annulus. Somite VIII is triannulate with the annular widths in the ratio of 1 : 3 : 2 ; whilst somite IX, although generally divided by two furrows to form three annuli with widths in the ratio 2 : 3 : 2, has an extra row of tubercles on the a_3 annulus, suggesting incipient subdivision. Somite X (Text-fig. 24B) is triannulate with its annular widths in the ratio of 2 : 3 : 1, the Xa_3 annulus being the first annulus of the clitellar constriction. Somites XI and XII are both biannulate and the annuli are generally of equal size. The male pore is situated mid-ventrally in the furrow between the two annuli of somite XI, while the female pore is similarly situated just posterior to the furrow dividing the two annuli of somite XII. Annulus $XIIIa_1$, which is small and sometimes difficult to see, is the last of the clitellar constriction. Somite XIII is quadriannulate, the ratio of widths being 1 : 3 : 2 : 1. Somites XIV to XXIV are also tetra-annulate,

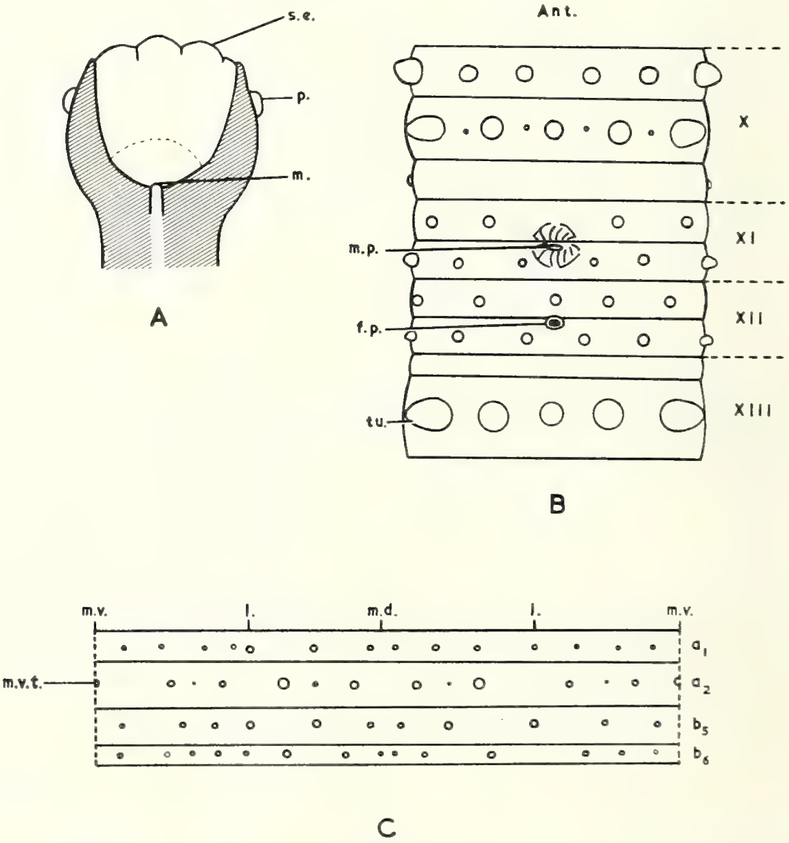


FIG. 24. *Pontobdella vosmaeri.* A. Section through anterior sucker, showing oral surface. B. Ventral surface of clitellar constriction, showing position of genital pores and tubercles. C. Tuberculation of typical quadriannulate somite split mid-ventrally. *m.v.t.*, mid-ventral tubercle ; *tu.*, tubercle ; See Fig. 11 (p. 406) for other abbreviations.

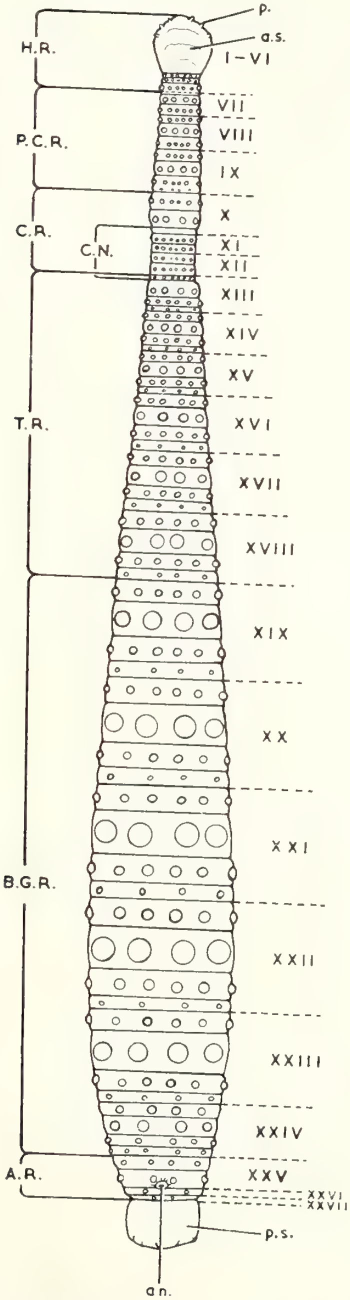
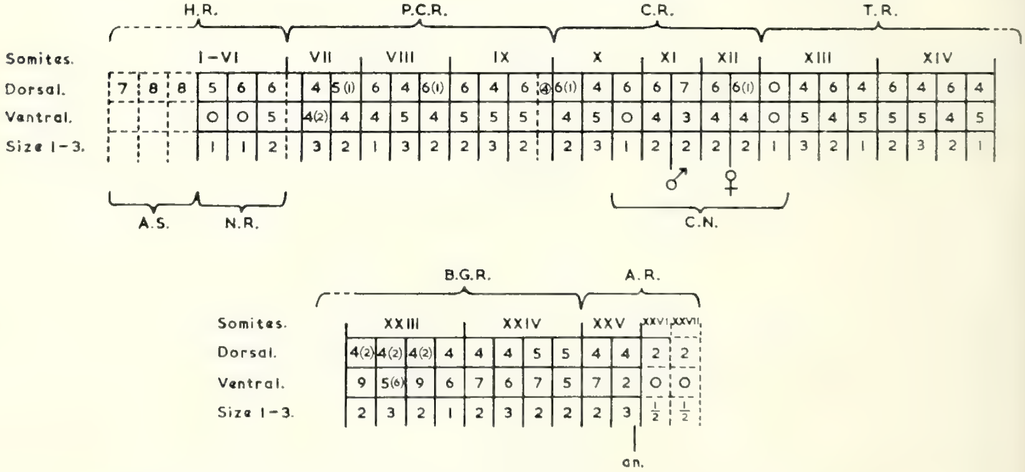

p.
a.s.
I–VI
H.R.
VII
VIII
P.C.R.
IX
X
C.R.
C.N.
XI
XII
XIII
XIV
XV
T.R.
XVI
XVII
XVIII
XIX
XX
XXI
B.G.R.
XXII
XXIII
XXIV
A.R.
XXV
XXVI
XXVII
p.s.
an.

FIG. 25. Dorsal view of *Pontobdella vosmaeri* showing annulation, tuberculation and suckers. See Fig. 12 (p. 407) for abbreviations.

but with the ratio of widths and tubercular sizes 2 : 3 : 2 : 1. The anal somites XXV–XXVII are much reduced. Somite XXV contains two annuli of which the posterior one is largest. Both somite XXVI and XXVII appear to consist of a single annulus each, the annuli being practically absent from the ventral surface. The anus occurs either in the furrow between somite XXV and XXVI, or near the posterior edge of the a_2 annulus of somite XXV.

TUBERCULATION (Text-fig. 26). The dorsal surface of the anterior sucker is sometimes marked by faint grooves, between which may occur seven to eight extremely small papillae. Tubercles on the first two annuli of the neck region are much reduced and generally absent from the ventral surface. Annulus IXa_3 has a double row of tubercles, in which the posterior row is by far the smallest. According to Rivière (1925) annulus Xa_3, the first annulus of the clitellar region, is non-tuberculate, but in some specimens it bears tubercles dorsally. On the other hand somite $XIIIa_1$ was according to Rivière tuberculate, but in some specimens it is non-tuberculate. As these annuli are small it may be expected that their tuberculation will vary.

Text-fig. 24C shows the tuberculation of a typical quadriannulate somite. Although the secondary tubercles on the a_2 annulus are subject to variation, the number of primary tubercles is constant. This species differs from *Pontobdella muricata* in having nine primary tubercles on the a_2 annulus, including one situated mid-ventrally. The a_1 annulus possesses about fourteen primary tubercles and a varying number of secondary tubercles, while b_5 has about twelve primary tubercles



Somites.				I–VI			VII		VIII			IX				X			XI		XII		XIII				XIV			
Dorsal.	7	8	8	5	6	6	4	5(1)	6	4	6(1)	6	4	6	④	6(1)	4	6	6	7	6	6(1)	0	4	6	4	6	4	6	4
Ventral.				0	0	5	4(2)	4	4	5	4	5	5	5		4	5	0	4	3	4	4	0	5	4	5	5	5	4	5
Size 1–3.				1	1	2	3	2	1	3	2	2	3	2		2	3	1	2	2	2	2	1	3	2	1	2	3	2	1

Somites.	XXIII				XXIV				XXV		XXVI	XXVII
Dorsal.	4(2)	4(2)	4(2)	4	4	4	5	5	4	4	2	2
Ventral.	9	5(6)	9	6	7	6	7	5	7	2	0	0
Size 1–3.	2	3	2	1	2	3	2	2	2	3	½	½

FIG. 26. Diagram illustrating the tuberculation of a single specimen of *Pontobdella vosmaeri*, anterior extremity above, posterior below. A.S., region of anterior sucker. The numbers in brackets in this diagram indicate a regular increase in numbers of tubercles found in this region in other specimens. Secondary tubercles are not indicated here because of their irregularity. " ½ " in the size column indicates the presence of small annulus dorsally only. Dotted lines indicate where additional annuli may or may not be present. See Fig. 13 (p. 409) for other abbreviations.

and up to six secondary ones, rarely having a total of more than fifteen. Annulus b_6 has about fourteen small tubercles. The large tubercles are generally conical, with up to eight apical sensillae, whereas small tubercles generally lack sensillae.

REMARKS. Herter (1935) suggested that *Pontobdella brumpti* Rivière (1925) appears to be synonymous with *Pontobdella vosmaeri* Apathy (1888). Although Rivière referred to Apathy, he did not mention the brief but adequate description of *P. vosmaeri*, which is placed in an addendum to the paper. It seems that Rivière overlooked this description, since he referred only to a brief description given by Blanchard (1893).

DISTRIBUTION. Plymouth, Roscoff, Capri.

HOST. Rays?

Pontobdella aculeata Harding, 1924

Pontobdella aculeata Harding, 1924 : 491.

DESCRIPTION. *General characters.* (Specimens not examined.) Body fusiform, attenuated anteriorly and circular in cross-section. Length 35–64 mm., breadth 6–8 mm. Colour dull grey to reddish brown, occasionally with linear spots on the a_2 annulus of each somite. Anterior sucker attached eccentrically, small, circular, with a corrugated edge, without papillae and apparently with no fringe. Anterior : posterior sucker ratio 1 : 1 or former slightly larger. Posterior sucker circular, with corrugated edge and attached centrally.

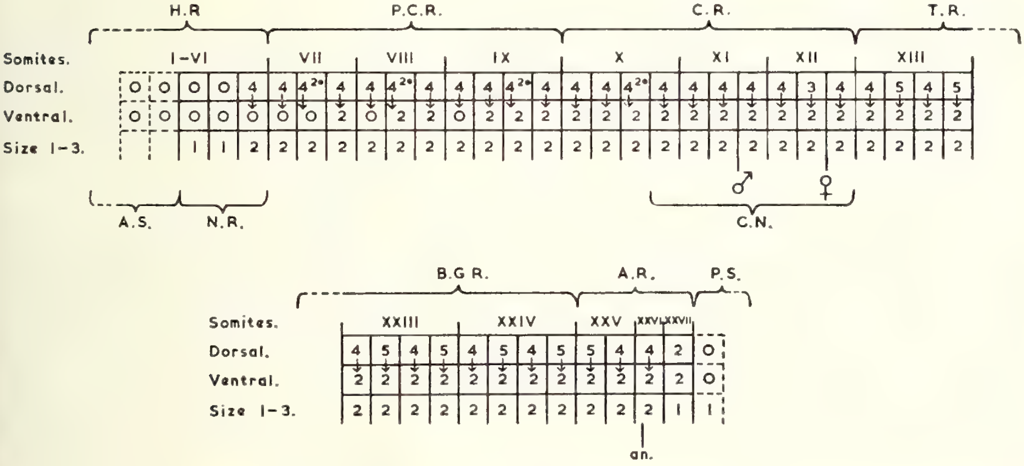

H.R
P.C.R.
C.R.
T.R.
Somites. I–VI VII VIII IX X XI XII XIII
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FIG. 27. Diagram illustrating the tuberculation of a single specimen of *Pontobdella aculeata*, anterior extremity above, posterior below. Compiled from the details in Harding (1924 and 1927). A.S., region of anterior sucker ; P.S., region of posterior sucker. Small number in top right hand corner of square, with a black dot, denotes number of brown spots on dorsal surface of leech. See Fig. 13 (p. 409) for other abbreviations.

ANNULATION. Uniannulate somites	XXVI, XXVII.
Biannulate somites	XXV.
Triannulate somites	VII, VIII, XI, XII.
Quadriannulate somites	IX, X, XIII–XXIV.

Annuli of quadriannulate somites approximately equal in width but becoming smaller towards the extremities of body. Dorsal surface of anterior sucker may possess faint furrows. Neck possesses three annuli with ratio of widths from anterior end 1 : 1 : 2. Clitellum inconspicuous, probably comprising annuli Xb_6 to $XIIIa_1$. Male pore opens mid-ventrally in furrow between XIa_2 and XIa_3. Female pore opens mid-ventrally in furrow between $XIIa_2$ and $XIIa_3$. Anus opens mid-dorsally on the annulus of somite XXVI.

TUBERCULATION. Text-fig. 27 shows tuberculation near the anterior and posterior extremities, derived from details given by Harding (1924 and 1927). All annuli of a quadriannulate somite possess lateral tubercles with the tubercles on b_5 largest. In addition, on the dorsal surface, the a_1 and b_5 annuli possess a paramedian pair, whilst the a_2 and b_6 annuli possess a para-marginal pair and a median tubercle. Ventrally there is only a para-marginal pair present on all annuli.

DISTRIBUTION. Bassein River, Burma; Gregory Isles, Mergui Archipelago, Burma; Wadge Bank, Ceylon (de Silva), 1963*a*).

HOST. Teleost *Harpodon nehereus.* (This fish is found in fresh water and estuaries as well as the sea.)

Pontobdella rugosa Moore, 1938

Pontobdella rugosa Moore, 1938 : 5.

DESCRIPTION. *General characters.* (No specimens examined.) Body slender, tapering gradually from the anterior to posterior end, length about 40·5 mm., maximum breadth 2·3 mm. and slightly flattened. Striking colour pattern metamerically blotched and annulated, with ground colour of ferruginous brown and pale yellow markings or vice-versa. The pattern varies considerably.

Anterior sucker sub-hemispherical, eccentrically attached so that oral surface faces ventrally, bearing a fringe (welt according to Moore), with fifty-two small papillae, two circles of sub-marginal papillae, and marked postero-dorsally by faint annulations, with rows of small papillae and pigment spots with vestigial eyes. Mouth situated centrally. Anterior : posterior sucker ratio 1 : 1·7. Posterior sucker cup-shaped when contracted, generally not exceeding the diameter of the body. Margin furrowed, cavity of sucker shallow, and externally rayed with brown rays.

ANNULATION. Uniannulate somites	XXVI, XXVII.		
Biannulate somites	XXV	XII.	XXIV.
Triannulate somites	(VI?) XI		
Quadriannulate somites	XIII–XXIII	VII–X	
Sexannulate somites			

Neck made up of four annuli, the first being small and reduced ventrally, the other three equal in size. Somites VII–X quadriannulate, with a_1 and a_2 tending to be biannulate. This tendency becomes more prominent posteriorly, as does the complexity and size of the somites. Clitellum ill-defined, probably extending from Xb_6 to $XIIIa_1$. Somite XI triannulate with annular size becoming slightly smaller posteriorly. Somite XII bi- or triannulate. Male pore on annulus XIa_2 and female pore in furrow between annuli $XIIa_1$ and $XIIa_2$ or as far forward as middle of annulus $XIIa_1$ (i.e. in furrow between $XIIb_1$ and $XIIb_2$). Somites XIII to XXIII are quadriannulate and the annular sizes are usually $a_1 > a_2 > b_5 = b_6$. In somite XXIV the furrow between b_5 and b_6 is often indistinct. Somite XXV is biannulate, with the anterior annulus largest. Anus mid-dorsal in furrow between somite XXVI and XXVII.

Tuberculation. Text-fig. 28 shows tuberculation of the anterior and posterior regions from details given by Moore (1938), but not including small secondary tubercles, although they are said to be present in varying numbers. Tubercles are generally largest dorsally, Particularly on a_1 annuli. They are small or absent on neck annuli, somite VII, the clitellar constriction (Xb_6–$XIIIa_1$), the anal region and b_6 of somites VIII–X. There are no tubercles on the small indistinct b_2 and b_4 annuli of somites VII–X. Otherwise dorsally, on all a_1, b_5 and b_6 annuli, there are two pairs of tubercles, outer paramedians and supra-marginals, while on a_2 annuli there are a lateral pair of tubercles and a pair near the intermediate line. Ventrally, a_1, b_5 and b_6 bear two pairs of (para-median and submarginal) tubercles, while a_2 bears a single pair on the intermediate lines. The tubercles are large, pointed, conical and with one or more apical papillae.

Distribution. Commonwealth Bay, King George V Land; 66° 32′ S., 141° 39′ E., 157 fathoms; 65° 42′ S., 92° 60′ E., 60 fathoms.

Host. Not recorded.

Genus ***PENTABDELLA*** gen. nov.

Type species. *Pontobdella dispar* Cordero, 1937.

Diagnosis. Tuberculate Piscicolidae in which most of the somites of the testicular and caecal regions are pentameric.

Pentabdella dispar (Cordero, 1937)

Pontobdella dispar Cordero, 1937 : 13.

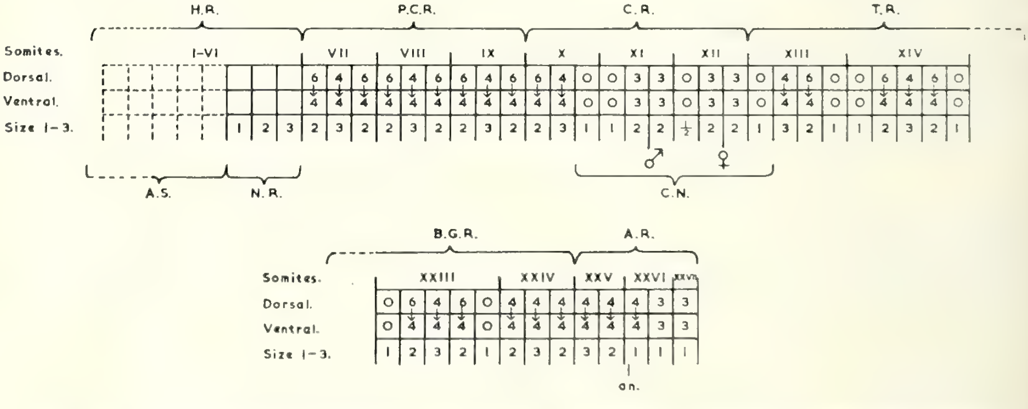
Description. *General characters.* The following description is based on that by Cordero. The body is fusiform, elongated, of circular section and a uniform pale yellow. It may be up to 160 mm. long (including suckers) and 16 mm. wide (about annulus $XXIa_2$). Anterior sucker hemispherical, smooth, convex externally and somewhat flattened laterally, with about five faint annulations near its base dorsally.

It possesses a marginal fringe bearing three pairs of papillae. The internal surface is concave and smooth. The anterior : posterior sucker ratio varies between 1 : 0·8–1 : 1·6, presumably depending upon contraction.

The posterior sucker is constricted at the base, convex and smooth externally, with a thick margin but no fringe. It does not generally exceed the maximum diameter of the body.

Annulation.	Uniannulate somites	XXVII	} XXVI.
	Biannulate somites	XXV	
	Triannulate somites	VII–XII, XXIV.	
	Quadriannulate somites	XIII.	
	Quinqueannulate somites	XIV–XXIII.	

The neck is made up of three annuli, of which the first is smallest while the other two increase in size posteriorly. The preclitellar somites are triannulate, increasing in size posteriorly with the central annulus largest. The first two annuli of somite X are similar to annuli in the preclitellar region, but annulus Xa_3 is smooth and much thinner, being the first annulus of the clitellar constriction. This is composed of eight annuli, including Xa_3 and $XIIIa_1$, all uniformly small. The male pore opens between annulus XIa_2 and XIa_3, and the female pore betwen $XIIa_2$ and $XIIa_3$. Annulus $XIIa_1$ is sometimes unrecognizable ventrally. The abdomen, from somite XIII to XXIV, is five times the length of the preclitellar and clitellar regions combined. Somite XIII is quadriannulate, with a_2 the largest annulus. Somites XIV to XXIII are quinqueannulate, with the ratios of the annuli b_1, b_2, a_2, b_5 and b_6 approximately 1 : 4 : 6 : 4 : 1. Somite XXIV consists of three annuli which are



Somites.	I–VI								VII			VIII			IX			X			XI			XII			XIII				XIV				
Dorsal.									6	4	6	6	4	6	6	4	6	6	4	O	O	3	3	O	3	3	O	4	6	O	O	6	4	6	O
Ventral.									4	4	4	4	4	4	4	4	4	4	4	O	O	3	3	O	3	3	O	4	4	O	O	4	4	4	O
Size 1–3.						1	2	3	2	3	2	2	3	2	2	3	2	2	3	1	1	2	2	½	2	2	1	3	2	1	1	2	3	2	1

Somites.	XXIII					XXIV			XXV		XXVI		XXVII
Dorsal.	O	6	4	6	O	4	4	4	4	4	4	3	3
Ventral.	O	4	4	4	O	4	4	4	4	4	4	3	3
Size 1–3.	1	2	3	2	1	2	3	2	3	2	1	1	1

FIG. 28. Diagram illustrating the tuberculation of a single specimen of *Pentabdella dispar*, anterior extremity above, posterior below. Compiled from the details in Cordero (1937). Size numbers 1–3 indicate smallest, middle and largest annuli respectively, of any somite, but they are related only to adjacent somites since size of annuli generally decreases towards the extremities. "½" in size column indicates the presence of a small annulus dorsally only. The dotted line indicates where annuli may or may not be present, while blank squares indicate where no information is given. See Fig. 13 (p. 409) for other abbreviations.

similar to the central three annuli of previous somites. Somite XXV, the first of the three anal somites, consists of two annuli, equivalent to a_2 and a_3 of previous somites, while the two annuli of somite XXVI are much reduced. Somite XXVII is uniannulate and very small, and the anus opens mid-dorsally on the a_1 annulus of somite XXVI.

TUBERCULATION. Text-fig. 29 is derived from the description by Cordero (1937). No details of tuberculation are given for the neck region. Each a_2 annulus of the preclitellar region has four pairs of mammilate tubercles with apical rosettes, one pair para-medianly on the dorsal surface, one pair laterally and two slightly smaller pairs ventrally. Annuli a_1 and a_3 possess five pairs of conical warts with apical rosettes, which are not as conspicuous as those on the a_2 annulus. In the clitellar constriction, annuli Xa_3, XIa_1, $XIIa_1$ and $XIIIa_1$ are generally smooth, while the other annuli are more wrinkled and bear six pairs of small sharply-pointed tubercles each. The b_1 and b_6 annuli of somites XIV to XXIII are smooth, while b_2 and b_5 possess ten mammilate tubercles each, four dorsal, two lateral and four ventral, the centro-ventrals being smaller than their neighbours. The a_2 annulus possesses eight large conical tubercles with rosettes at their summits, two dorsally, two laterally and four ventrally. Annuli $XIIIa_2$, b_5 and b_6 have similar tuberculation to somite XIV. The tuberculations of annuli a_1 to a_3 of somite XXIV are similar to b_2, a_2 and b_5 of previous somites and the first and second annuli of somite XXV are similar to a_2 and a_3 of somite XXIV. The a_1 and a_2 annuli of somite XXVI have eight and six tubercles respectively, while the single annulus of somite XXVII has about six tubercles. Small secondary tubercles may be dispersed between the larger tubercles and may even occur in the furrows.

DISTRIBUTION. 34° 50′ S., 52° 20′ W., 58–65 fathoms ; Ilha Rasa, 80 metres depth.

HOST. Not recorded.

*GENUS ET SPECIES INQUIRENDAE**

Pontobdella rayneri Baird, 1869

Pontobdella rayneri Baird, 1869 : 313.

DESCRIPTION *after Baird.* Body cylindrical, attenuated anteriorly. Annuli with tubercles which have sensillae at summit. Preclitellar region twelve tuberculate annuli. Clitellum five tuberculate annuli. Anterior sucker small, circular, with three pairs of papillae on margin and large brown triangular pigment patches. Posterior sucker largest, rayed with brown and with puckered margin. On body, every third row of tubercles is largest. Length 1 inch.

On re-examination of this material it was also found that the posterior sucker was joined to the body by quite a narrow waist ; however the material was in too poor a condition to improve on this description. This species is almost certainly a member of the genus *Stibarobdella*.

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* Including *Orientobdella japonica* (Vasiliev), see p. 439.

Pontobdella leucothela Schmarda, 1861

Pontobdella leucothela Schmarda, 1861 : 6.

Description *after Schmarda.* Body circular with tubercles on back and sixteen trimeric somites. Neck fifteen annuli. A_2 annuli broadest, with four semi-conical tubercles. Colour yellowish grey, tubercles white. Length 18 mm. This species is apparently a member of the genus *Stibarobdella.*

Distribution. Port Jackson, New South Wales.

Host. Not recorded.

Pontobdella prionodiscus Schmarda, 1861

Pontobdella prionodiscus Schmarda, 1861 : 7.

Description *after Schmarda.* Body cylindrical, length 48 mm. and breadth 10 mm., attenuated at each end, tuberculate and a dirty green with a little yellow and brown coloration. Anterior sucker with sixteen rounded tubercles and with eight papillae on the rim. Anterior : posterior sucker ratio 1 : 1·6. Posterior sucker bell-shaped.

Said to have some similarities to the quadriannulate form *Pontobdella spinulosa,* which is now a synonym of *Pontobdella muricata.*

Pontobdella tatejamensis Oka, 1910

Pontobdella tatejamensis Oka, 1910 : 171.
Parapontobdella tatejamensis : Harant, 1929 : 650.

Description *after Oka.* Body elongated, fusiform, posterior middle half of body expanded like abdomen. Red brown to dark green. Tubercles weakly developed. Suckers small. Lateral vesicles indistinctly recognizable externally. Length of body up to 2 cm., breadth up to 3 mm.

This description gives no sound evidence for placing the leech in the genus *Pontobdella.*

Distribution. Hondo ; Awa, Suruga, Sagami.

Host. Teleost.

Pontobdella oligothela Schmarda, 1861

Pontobdella oligothela Schmarda, 1861 : 6.

This species does not belong to the Pontobdellinae since it possesses numerous salient pulsatile vesicles which the latter lack. The rough white patches described on the dorsal surface of somite 10, 11, 14 and 17 on fresh specimens seem to indicate, according to Blanchard (1894) and Harding (1910), that the species is probably identical with *Trachelobdella lubrica* Grube, 1840 : 60, (*Pontobdella littoralis* : Johnston, 1865 and *Pontobdella campanulata* : Johnston, 1865, pp. 42 and 304 were also probably *Trachelobdella lubrica*).

Pontobdella vittata de Blainville, 1828

Pontobdella vittata de Blainville, 1828 : 557.

Not one of the Pontobdellinae because it possesses no tubercles and probably has biannulate somites.

OPHIBDELLA Beneden & Hesse, 1863

Ophibdella labracis Beneden & Hesse, 1863 : 25.

The specimen described under this generic name had no tubercles, yet Apathy (1888) believed it was a young Pontobdellinid. However, the hatching young of *Pontobdella muricata* are similar to the adults except in size, so presumably *Ophibdella* should remain a separate genus.

KEY TO THE SPECIES IN THE SUBFAM. PONTOBDELLINAE

1	Abdominal somites triannulate	Gen. ***STIBAROBDELLA*** 2
–	Abdominal somites quadriannulate	Gen. ***PONTOBDELLA*** 9
–	Abdominal somites quinqueannulate	***Pentabdella dispar*** (p. 433)
2	Anterior sucker with a marginal fringe	***Stibarobdella loricata*** (p. 413)
–	Anterior sucker without a marginal fringe	3
3	Anterior sucker with a pigment patch or patches	4
–	Anterior sucker without pigment patches	7
4	Anterior sucker with no papillae	***Stibarobdella taprobanensis*** (p. 421)
–	Anterior sucker with papillae	5
5	Anterior/posterior sucker ratio between 1 : 2 and 1 : 3	***Stibarobdella macrothela*** (p. 405)
–	Anterior/posterior sucker ratio between 1 : 1 find 1 : 2	6
6	Anterior sucker with two distinct pigment patches and anterior/posterior sucker ratio approximately 1 : 1 or latter slightly larger	***Stibarobdella bimaculata*** (p. 415)
–	Anterior sucker with single triangular pigment patch and anterior/posterior sucker ratio approximately 1 : 1.5	***Stibarobdella tasmanica*** (p. 420)
7	Anterior sucker with papillae	8
–	Anterior sucker without papillae	***Stibarobdella moorei*** (p. 422)
8	9 tubercles including a mid-ventral tubercle, on the a_2 annulus	***Stibarobdella planodiscus*** (p. 418)
	6 tubercles on a_2 annulus 4 dorsally and 2 ventrally	***Stibarobdella australiensis*** (p. 422)
9	Anterior sucker with fringe or welt	10
–	Anterior sucker without fringe	11
10	Anterior sucker without pigment patches but with 3 pairs of papillae, anterior/posterior sucker ratio 1 : 1 or former slightly larger	***Pontobdella muricata*** (p. 423)
—	Anterior sucker with a pair of pigment patches and 52 marginal papillae and 2 submarginal rows of papillae, anterior/posterior sucker ratio approximately 1 : 1·7	***Pontobdella rugosa*** (p. 432)
11	Anterior sucker with 3 pairs of papillae, anterior/posterior sucker ratio between 1 : 1.5 and 1 : 2	***Pontobdella vosmaeri*** (p. 427)
—	Anterior sucker without papillae, anterior/posterior sucker ratio 1 : 1 or former slightly larger	***Pontobdella aculeata*** (p. 431)

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ADDENDUM

In preparing this review I unfortunately overlooked two species which are important for problems of annulation and affinities of the Pontobdellinae.

The first, *Pontobdella biannulata* Moore (1957. Hirudinea. *Rep. B.A.N.Z. antarct. Res. Exped.* 1929–1931. Ser.B, **6** (6) : 99–105) has two annuli per urosome somite. It may now be placed tentively in *Stibarobdella* if the definition of that genus is widened to include tuberculate leeches with either three or two annuli per urosome somite.

The other species, *Pontobdella japonica* Vasiliev (1939. The Ichthyobdellidae of the Far East. *Works of the Karelian State Pedological Institute*, **1**, Biol. Ser., (1) : 25–68), has fourteen annuli per urosome somite and is now the type of *Orientobdella* Epshtein (1962. A survey of the fish leeches (Hirudinea, Piscicolidae) of the Bering Sea, the Sea of Okhotsk and the Sea of Japan. *Dokl. Akad. Nauk SSSR*, **144** (5) : 1181–1184). Although tuberculate, it has quite large lateral vesicles and it seems doubtful whether it should be included in the Pontobdellinae.

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National Institute of Oceanography

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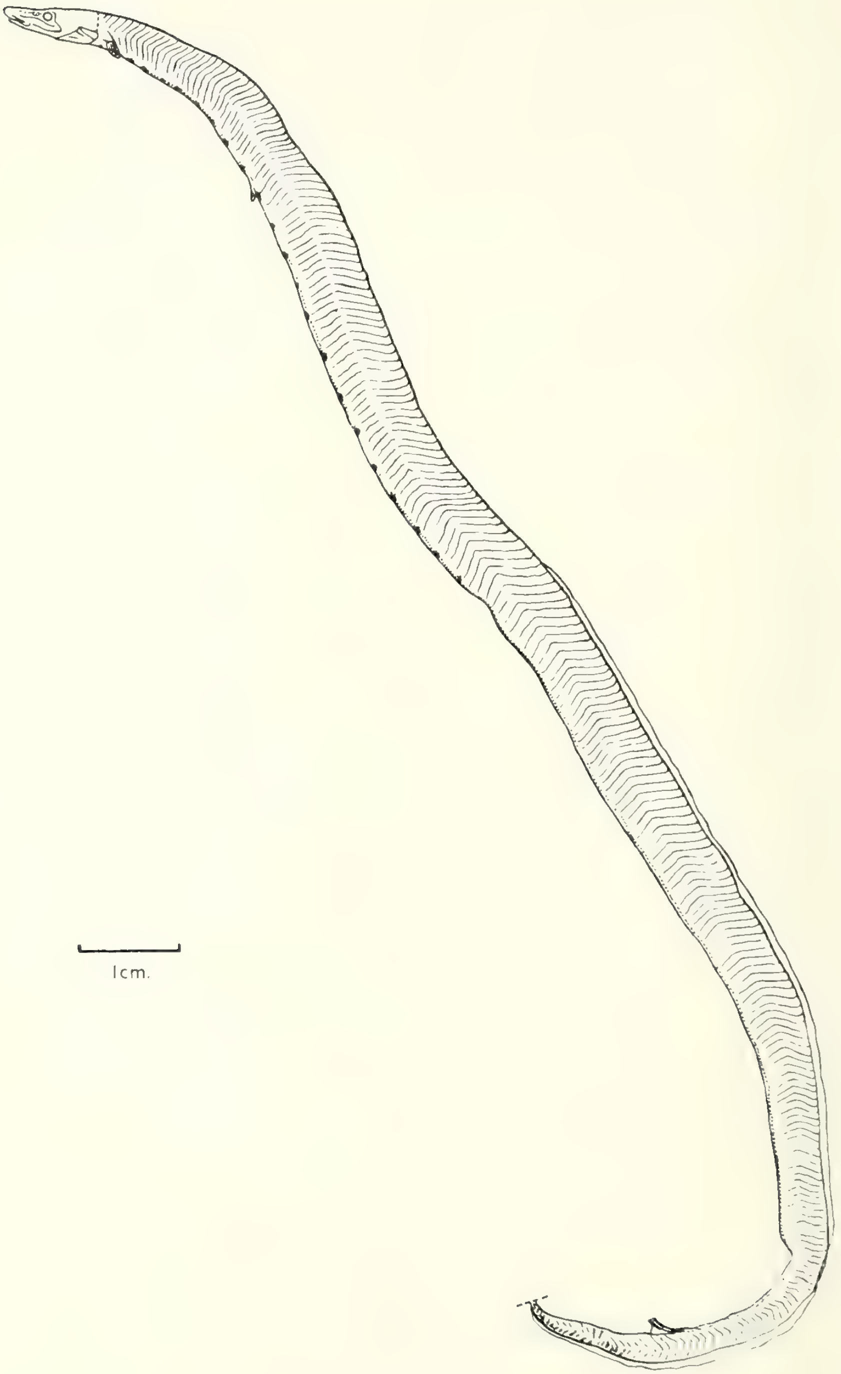

FIG. 1. Whole leptocephalus of an *Aldrovandia* sp. captured off Madeira.

ON THE FIRST HALOSAUR LEPTOCEPHALUS: FROM MADEIRA

By C. M. H. HARRISSON

INTRODUCTION

During the autumn of 1961 the R.R.S. Discovery made a series of collections in the Canary Basin of the North Atlantic. Among the fishes examined in the spring of 1964 was an elongate larva taken by an Isaacs-Kidd midwater trawl towed for 2 hours at a mean depth of 1100 m. (601·5 fths.) and a position between 29° 59′ N., 22° 56′ W. and 29° 50′ N., 22° 57′ W. This larva strongly resembled one of the larger ribbon-like eel leptocephali, though after preservation for 2½ years in formalin and subsequent transfer to 70% alcohol, it was somewhat less transparent and of a yellowish tinge. The presence of a pair of small ventral fins combined with the highly characteristic pattern of opercular bones and head canals indicate that it can only be a halosaur. It is indeed the earliest developmental stage yet known for this curious group of largely benthic deep sea fishes.

DESCRIPTION

The larva (Text-fig. 1) is 190 mm. in length though the tip of the " tail " is missing. The original length must have been at least 3 or 4 mm. more. The head is small, 9·5 mm. from snout to basis cranii, 3·5 mm. in maximum depth. The body is flat and ribbon-like, with a gradual dorsoventral broadening behind the head, reaching its greatest depth (7·3 mm.) well behind the ventrals, then tapering away again gradually to the tip of the tail. There are some 250 myotomes, but an exact count is made difficult as the tail is damaged, and the myotomes become less distinct posteriorly. Each myotome consists of a simple V whose apex points forwards (Text-fig. 1). Damage also leaves intact epidermis only on the head, and for a short distance along the body beyond the level of the pectorals (Text-fig. 2). Over this whole area the skin is lightly speckled with black pigment. Summarizing the body proportions, the head length is contained some 20 times in the length and 3 times in the distance from the snout to the origin of the ventral fins, while the maximum body depth is twice the maximum head depth.

The fins consist of (i) a pair of pedunculate pectorals, set somewhat below the mid-line of the lateral profile, and with 10 rays, (ii) a pair of ventrals with 8 rays, and (iii) a larval fin-fold commencing a long distance behind the insertion of the ventrals and confined entirely to the dorsum. The " anal papilla " is close to the tip of the tail, at the level of the 207th myotome, and there is no sign of an anal fin-fold whatsoever, though it must be remembered the tip of the tail is missing. The branchiostegal rays are 10 in number, and there are 9 rakers, 1 on the upper, and 8 on the lower limb of the 1st gill arch. The ray formula so far as can be ascertained is thus: B 10; D —; P 10; V 8; A —.

The head is roughly conical, tapering forwards to a pointed snout that overhangs

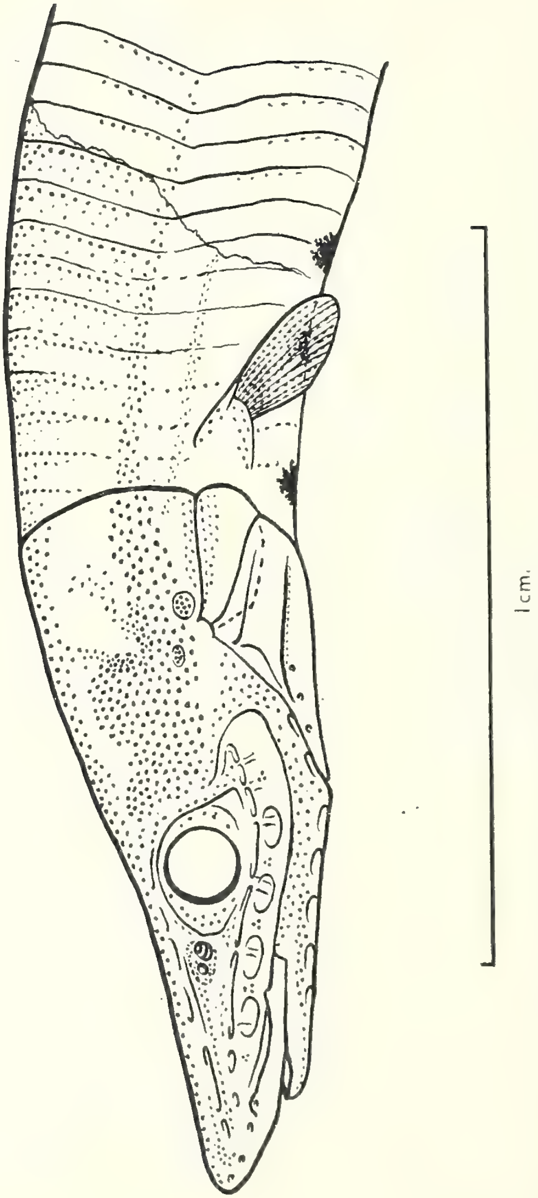

Fig. 2. Head of *Aldrovandia* leptocephalus enlarged to show details of lateral line canals and opercular structure.

the mouth. There are a number of tiny rounded mucus pores on the snout, while a series of pale elongate ovals marks the position of the supraorbital lateral-line canal. A pore just anterior to the nasal capsule marks the posterior limit of the adnasal canal. Much more conspicuous is the very large suborbital canal. Seen by transmitted light the neuromast cushions are visible as opaque dots and above each of these organs in the lateral canal wall is a pale elongate elipse, representing the curled dorsal edge of a developing lateral line scale. Seven such scales are visible, the most posterior, the smallest, lies at the point where the suborbital canal turns upwards behind the eye. Alternating with the cushions are large oval pores connecting the exterior with the canal lumen. A similar series of pores (likewise difficult to see owing to the transparency of the membrane they perforate), marks the position of the mandibular canal. There are no signs of the lateral line along the body. The opercular apparatus (Text-fig. 2) consists of a small shoulder-blade shaped operculum, partly overlain by a very large preoperculum which is perforated by endings of the VIIth cranial nerve. The suboperculum is a narrow splint of glassy transparency lying along the lower border of the operculum. The interoperculum is a slender rod passing from the suboperculum to the hind border of the mandible. It is connected to the " epihyal ". The suspensorium slopes obliquely upwards to the otic capsule, the dorsal end of the hyomandibular being roughly triangular and having a horizontal edge. The head was somewhat damaged on the right side and the operculum torn outwards allowing an internal view of the opercular apparatus. The lens of the right eye is missing. The left eye remains in better condition, and the diameter of the spherical lens closely approximates to the interorbital width across the frontals. The nasal capsules are placed immediately anterior to the orbits. The nasal rosette has 8 leaflets arranged in pairs. After clearing in glycerine, the structure of the auditory capsule became distinct. Three pale zones, and 2 clearly marked dark zones with the beginnings of a third, were seen in the otoliths.

Turning to details of the body characters there is a conspicuous row of large ventral melanophores spaced at intervals of about 1 pair to every third pair of myotomes, though more closely spaced at the anterior end and more widely separated at the posterior end of the series (Text-fig. 1). These pigment spots discontinue close to the level of the insertion of the dorsal fin-fold. Along the ventral edges of the myotomes is a series of small black dots, while similar minute dots of pigment are arranged close to the myotome septa above the mid-line of the body. This pigmentation is apparently subepidermal (vide supra). There are no signs of developing scales. It is difficult to make out accurate details of the course of the gut, of the kidneys and blood vessels, due to the semi-opacity of the myotomes. Although the viscera are still largely displaced below the body segments, the upper surface of the gut is partly hidden. A thorough examination could not therefore be undertaken without doing what was considered as excessive damage to the specimen. From the partial details visible it seems probable that the duct opening on to the anal papilla is the renal duct. The gut appears to end blindly some 22 segments more anteriorly.

LEPTOCEPHALUS FEATURES AND METAMORPHOSIS

Having described the chief morphological characters, the general importance of the discovery of this larval halosaur may now be considered. Following a discussion comparing modes of development in various groups of fishes, the characters of adult halosaurs will be compared with features in the larva, with a view to interpreting structures from a morphogenetic viewpoint, as well as to consider the larva's probably systematic position.

There is a series of " soft-finned " fishes, including the Tarpons and Lady-fishes (*Tarpon, Elops*) ; *Pterothrissus* ; the banana fish and bone fishes (*Albula, Dixonina*) ; the eels (*Apodes*) ; and the gulper eels (*Lyomeri*), all of which have a larval stage referred to as a *Leptocephalus*. The question is, whether the halosaurs also have a larva of this rather special type. To enlarge on this, one must first establish what particular features distinguish a *Leptocephalus* from other sorts of larva, then see which of these characters the only available halosaur larva has.

The first description of a *Leptocephalus* was that given by Gronovius in his *Zoophylacium* of 1763. He describes specimens taken in the Irish sea near Holyhead, Anglesey, by William Morris and sent to him by Thomas Pennant. The characters Gronovius gives in his latin diagnosis are : a scaleless body and head, laterally flattened, large eyes and mouth, as well as a long dorsal fin fold. Subsequent to the studies of Delage (1886), and Grassi & Calandruccio (1893) it was realized that the leptocephalus described by Gronovius was in fact a larval eel, while the classical work of Johannes Schmidt made known in great detail the developmental history of *Anguilla*. Later, it was found that the fishes of the groups mentioned above also have transparent larvae, with small pointed heads which are dorsoventrally much narrower than the greatly flattened body. Like eel leptocephali, such larvae also have a long dorsal fin-fold, an anus close to the tip of the tail and large larval teeth borne by the membrane-bones of the jaws. Probably in all, the space between the two lateral myotome sheets, above and below the notochord and bounded ventrally by the low-slung viscera, is filled with an acellular gelatinous tissue, as found by Rasquin (1955) in larval *Albula*. The above, then, may be taken as basic morphological characters common to all leptocephalus larvae.

The halosaur larva has a long and greatly flattened body. Like established leptocephali, it too has a small pointed head. Its anal papilla is close to the tip of the tail, and there is a long dorsal fin fold, while the body broadens to a maximum dorsoventral extent of more than twice the head depth. The simple myotomes form a ribbon down each flank of the body. Above the notochord, and between the nerve chord and the gut, the space is occupied by a gelatinous mass. Only two leptocephalic characters are absent : the transparency of the body and the large larval teeth. The specimen under consideration was yellowish and translucent, but not transparent or glassy-hyaline as are typical leptocephali. However, many Indo-Pacific eel leptocephali are similar to this in appearance, and moreover resemble the halosaur larva in having a ventral series of dark spots. The absence of teeth seems readily understandable if it is assumed that the halosaur larva has just reached the stage at which it is beginning metamorphosis. This contention is greatly strengthened by the following evidence.

In the great majority of fishes the larval period is a short one, lasting a matter of a few weeks. Prolonged " infantilism " is perhaps a general feature of fishes with leptocephalus larvae. At all events, in *Anguilla anguilla* the leptocephali are in their third year when metamorphosis begins (Schmidt, 1935). They then lose their larval teeth, while the body, following changes in the head, becomes more slender and less leaf-like. It is thus of great interest to find in this halosaur larva with a head of rather adult appearance, and strangely larval body, that the otoliths have three rings. If these are indeed annual rings, then not only does the developmental pattern seem similar, its timing too is alike in both eels and halosaurs. To recapitulate, there is evidence to suggest that the larva to hand was just beginning metamorphosis after a life span of three years. Probably a younger larva would have had large teeth as well as a more transparent and even more leaf-like body. There thus seems excellent justification for stating that the larval halosaur is a leptocephalus.

In the general description, it was remarked that the gut may have ended blindly. This may seem surprising. However one of the features of metamorphosis from the leptocephalus both in eels and elopoids (though probably not in Lyomeri) is the remarkable shift forward of the position of the anus. Bertin (1926), for example, records a shift of some 245–345 myotomes in *Nemichthys scolopaceus*. Now at this period the leptocephali stop feeding. Rasquin (1955) thinks that in *Albula* the gelatinous tissue between the myotome sheets provides the necessary reserves at metamorphosis, and until feeding begins again. This is probably true for other leptocephali. It would not therefore seem strange in a metamorphosing larva to find that the non-functioning gut pinched off a posterior section before retracting, and re-establishing the anus in its definitive position. It seems possible that this is what is happening in the halosaur larva. Alternatively, what appears to be the blind ending of the gut may ultimately prove to be merely a gastric caecum or hepatic lobe. Further material is required before this can be satisfactorily decided. Through the kindness of Mr. Alwyne Wheeler I was able to examine a number of X-ray photographs of adults of 7 species of Halosaur and in all the anus occurs at the level of the 55th–74th vertebra (see Table I, which is further discussed on p. 458). Assuming that the larval halosaur had an anus opening on the anal papilla, at the level of the 207th myotome, there must be a shift in the position of the anus of some 140 myotomes in amplitude during the change from larva to adult. Similar hypermetamorphic phenomena must therefore occur in both nemichthyid eels and halosaurs.

A fuller discussion of the processes occurring at metamorphosis in the halosaurs can only be made after a comparison of larval and adult features. The topic will be resumed after an account of the morphological characters which serve to identify the larva.

TABLE I

a. *Adult Segmentation Taken from Vertebral Numbers in Radiographs*

Genus and species	Material examined	Standard length (mm.)	Segment numbers: Anterior to pectoral fins	Anterior to ventral fins	Anterior to dorsal fin	Anterior to anus	Anterior to anal fin	Post-cephalic total
Halosaurus Johnson *ovenii* Johnson, 1863	Holotype B.M.N.H.	440 (465)	10	37	45	***74***	76	***274***
johnsonianus Vaillant, 1888	Paratypes B.M.N.H.	381 334+	8 8	31 31	39 39	***62*** ? ***66*** ?	64 68	***265*** ***223***+
Average number of preanal segments for the 2 spp examined :						***69***		
Aldrovandia Goode & Bean *rostrata* (Günther, 1878)	Holotype B.M.N.H.	495 (507)	8	38	46	***64***	66	***320*** ?
affinis (Günther, 1877)	Syntypes B.M.N.H.	420 410 (both 421)	8 10	36 36	39 38	***61*** ***64***	66 66	***252***
macrochir (Günther, 1878)	Lectotype B.M.N.H.	535 (545)	10	36	37	***61***	64	***260***
phalacra (Vaillant, 1888)	Paratype B.M.N.H.	207+	9	32	40	***60*** ?	62	***169***+
mediorostris (Günther, 1887)	Holotype B.M.N.H.	445 (444)	9	27	35	***55***	56	***216***
Average number of preanal segments for the 5 spp. examined :						***61***		

b. *Larval Segmentation Taken from Myotome Counts*

Genus and species	Material examined	Standard length (mm.)	Segment numbers: Anterior to pectoral fins	Anterior to ventral fins	Anterior to dorsal fin	Anterior to anus	Anterior to anal fin	Post-cephalic total
?	Larva from Discovery collections IKMT 4746	190	7	38	Only fin-fold present	***207***	Anal fin absent or missing	***250***+

The larva has ***207*** preanal myotomes. The maximum number of preanal vertebrae found in the adults above was ***74***, the minimum ***55***. It thus seems that the anus migrates over 133–152 segments at metamorphosis.

THE OPERCULAR STRUCTURE AND ITS DEVELOPMENT

In comparing characters shown by the larva with those of adult halosaurs, one may begin with features of the opercular structure and the head canals of the lateral line system. These are the most salient features indicating that this is indeed a halosaur. Adult characters seem well established in the head region long before the body assumes its definitive form.

Taking first the opercular structure. Marshall (1962) has disentangled from a century's terminological controversy the true relation of the opercular bones in halosaurs by examining an *Aldrovandia macrochir*. He showed that all the usual opercular bones are present in halosaurs, but that the preoperculum grows back in the opercular fold to cover the suboperculum and the interoperculum more or less completely. Superficially only two bones are visible, a small upper disc, the operculum, and a large lower flange, the preoperculum (Text-fig. 4*c*). This condition, clearly visible in the larva (Text-fig. 2), is unique among fishes. It seems worth a short digression to discuss it in detail.

The fish operculum is a functional unit acting as a respiratory valve and pump (Hughes, 1960), and as a linking mechanism allowing small muscles of the hyoid plate (adductor operculi, Edgeworth, 1935) to help open the lower jaw (van Dobben, 1935). The (dermal) bones are, however, of two sorts : (i) the preoperculum which develops in relation to the lateral line and (ii) the " truly opercular " bones related solely to " cartilage bones " of the hyoid arch. The operculum articulates to a process on the hyomandibular. The suboperculum is often attached to the operculum, but in Mormyrids it is hard to distinguish it from a branchiostegal ray and in *Engraulis* it is even connected to the epihyal, increasing its resemblance to a branchiostegal ray (Ridewood, 1904 : 75). This raises the question of the development of the bones. If branchiostegal rays develop as procartilaginous rudiments can they be equated with plates of bone held not to do so? The operculum first appears as a cartilage in eels (Norman, 1926), and the evanescent rudiment in lyomerous larvae is also cartilaginous (Orton, 1963), which suggests they can. There is then the interopercular : commonly it is displaced anteriorly as a triangle of bone. According to van Dobben (l.c.) it is often connected to the interhyal (stylohal). In *Elops* (Ridewood, 1904) the branchiostegal rays all develop into flattened plates of bone so there is a continuous series of similar ossifications from the operculum downwards, but the anteriorly displaced interoperculum does not appear to belong with this series of bones. It is thus interesting to note that in the halosaur larva the interoperculum (Text-fig. 5) develops with all the appearance of a branchiostegal ray. It is attached to the epihyal, with its upper end connected to the suboperculum, and linked to the hind end of the lower jaw by a slip of muscle, and a tendon which is shown in Günther, 1887, pl. IX, fig. 2, labelled " lig ". In adult Halosaurs the interoperculum flattens out and enlarges to become a paddle shaped bone (Text-fig. 4*a*). Morphologically then, the interoperculum seems equivalent to a branchiostegal ray. Its forward displacement in many fishes is explained if one accepts that it most often belongs to that part of the hyoid arch kinked anteriorly as the interhyal. The connection of the interoperculum with the epihyal in halosaurs is thus unusual. In *Anguilla* elvers, too, the interoperculum is paddle-shaped (Text-fig. 3). Further, in eels the opercular fold is supported largely by the branchiostegal rays (Regan, 1912), while the operculum and suboperculum are small. Except for the large preoperculum, the halosaur opercular structure thus resembles the condition found in the eels. The details seen in the larva and described above, correspond closely with those given by Marshall (1962), for an adult halosaur.

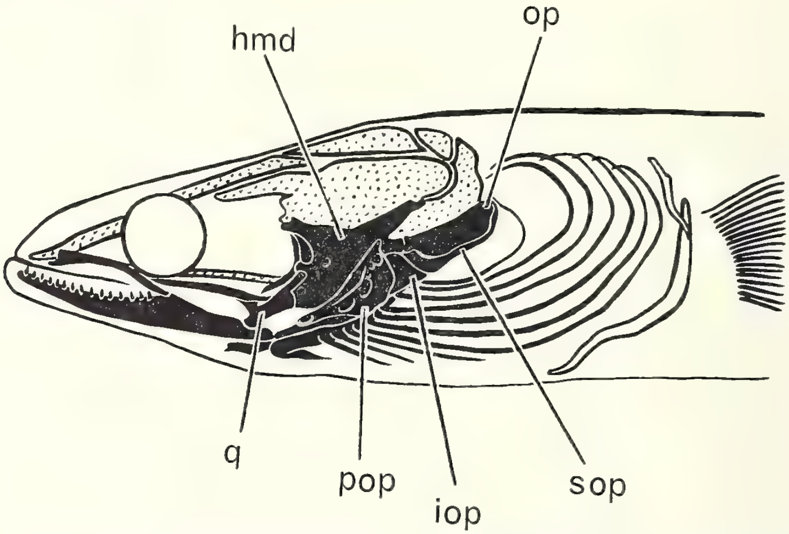

FIG. 3. Head of an *Anguilla* elver showing the bone structure. *hmd.* = hyomandibular, *op.* = operculum, *sop.* = suboperculum, *iop.* = interoperculum, *pop.* = preoperculum, *q.* = quadrate.

THE PREOPERCULUM AND THE HEAD CANALS

The preoperculum may best be considered in relation to the head canals of the lateral line series. Its great size in halosaurs (and in these fishes it has secondarily become the chief support of the opercular fold) seems related to the enormously enlarged mandibular canal (and not to the infraorbital canal as Marshall, 1962, stated). There is no connection between infraorbital and mandibular canals. Figures (pl. LXXXIV : 3–6) by Garman (1899) are misleading in this respect ; they suggest a jugular connection, present in Dipnoi but not known in any Actinopterygian.

The thin walled and greatly expanded canals in the preopercular region are delicate and often damaged in preserved material. In the larva the infraorbital canal stops short of the preoperculum, terminating in a backwardly directed bulge (Text-fig. 2). In several adult *Aldrovandia* examined, the infraorbital canal just extends on to the preoperculum to end blindly in a series of finger-like processes, adhering closely to the preopercular membrane and the wall of the mandibular canal

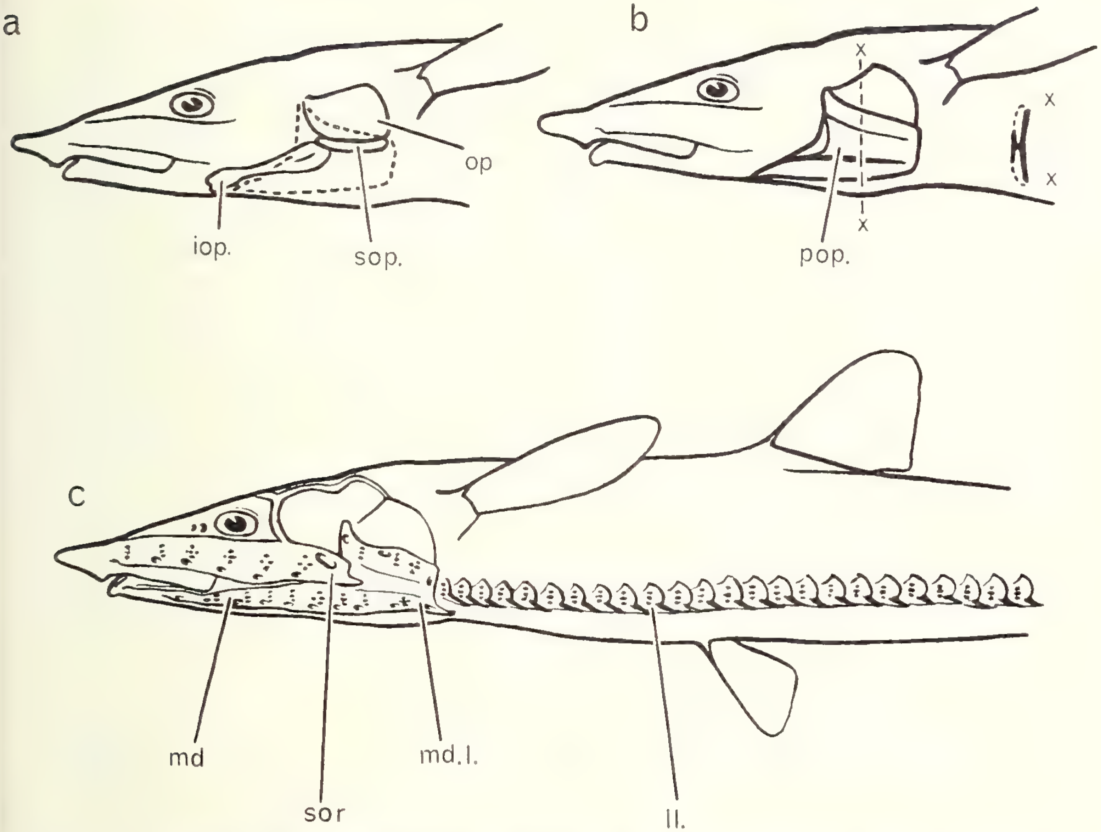

Fig. 4. Diagrams of adult *Aldrovandia* showing features of the lateral line and opercular structure (after Gilbert, 1905). (a) head with preoperculum as stippled outline. *iop* = interoperculum, *sop.* = suboperculum, *op.* = operculum. (b) head with inset vertical section ×——× of the preoperculum = *pop.* (c) head and anterior part of body *md.*=mandibular canal, *sor.*=suborbital canal, *md. l.*=preopercular loop of mandibular canal, *l.l.*=lateral line along body.

below (Text-fig. 4). The larval mandibular canal is evident from the series of large pores along the underside of the lower jaw. It curls round the end of the jaw on to the preoperculum, but further detail is obliterated by damage. In adult *Aldrovandia* the mandibular canal curves back in a broad loop, over the main preopercular flange, and is partly overlain by a thin lamina of bone. This lamina is connected by a delicate strut to the main preopercular flange. The preoperculum thus has an I-girder cross-section with the outer lamina smaller than the main flange (Text-fig. 4*b*). Probably the lamina arises from the fusion back-to-back of two series of curled scale-like ossifications (similar to those in the suborbital canal), formed in the wall of the preopercular loop of the mandibular canal, and additionally fused basally to the flange. The lamina is clearly visible in the larva, as is a part of the canal which, in the adults, was seen to narrow above the loop, and open to the surface by a large pore near the upper margin of the preoperculum. It is evident that the extraordinary size of the preoperculum may be correlated in part with the unusually developed lateral-line canal normally associated with this bone. The outline of the bone corresponds with the shape of the canal-loop. Neuromast cushions of the lateral-line system develop in relation to endings of the facial, glossopharyngeal and vagus nerves. The backward growth in the opercular fold of numerous branches of the ramus hyomandibularis of the facial, may explain the origin of this loop. The differences in opercular structure between halosaurs and eels can thus be related to the development of the giant lateral line canals and the unusually rich innervation of the opercular fold in the former group of fishes.

Little more detail of the larval head-canal pattern can be seen than has been described above. The suborbital and mandibular canals are clear, and the rostral commissure is apparent from pores on the snout. Gosline's account (1961) of the arrangement in an adult *Aldrovandia*, may be compared with Text-fig. 2 showing the larval head.

THE GENERIC AND SPECIFIC IDENTITY OF THE LARVA

Beyond characters general to the family Halosauridae, there remains a restricted range of features useful at the generic and specific level for attempting to determine the larva. A consideration of the significance of certain adult features seems a necessary corollary in the following discussion.

Since Johnson's description in 1863 of the first halosaur, 24 other forms have been named, and published records and descriptions of very various excellence have appeared covering a total of over 400 specimens, more than 300 of which are from the Atlantic. The rest are from localities scattered through the tropical and subtropical regions: The Prince Edward Islands (Günther, 1878), the Indian Ocean, (Alcock, 1889–98; Brauer, 1908; Norman, 1939), the Malay Archipelago (Weber, 1913), South Australia (McCulloch, 1926), The Philippines (Fowler, 1933), Japan (Günther, 1877, 1887), Hawaii (Gilbert, 1905), and the Gulf of Panama (Garman, 1899). Additional observations have been made from bathyscaphes and by deep-sea photography [e.g. Pérès (1956), Houot (1958)]. Further details are given in Table III, in the map, Text-fig. 6, and in the Gazetteer (Appendix pp. 475–486). There has, however, been no recent review of the family Halosauridae.

Vaillant in 1888 after studying the material brought back by the "Talisman" divided the genus *Halosaurus* into 2 groups according to whether or not the interorbital width was greater than the horizontal diameter of the eye. Vaillant's group of species with a large interorbital width was also characterized by lacking scales on the vertex of the head. His other group, those with a narrow interorbital width, contained, apart from his new species *phalacrus*, only species with a scaly vertex. Goode & Bean (1895) used the criterion of scaled as against scaleless vertices to divide the halosaurs, placing Vaillant's *phalacrus* in their new genus *Aldrovandia*, along with the other smooth-headed species. Now the type of *Aldrovandia phalacra* was slightly smaller (430 mm.) than previously described species and is perhaps a species generally characterized by small size. One is led, further, to wonder whether interorbital width in *Aldrovandia* does not increase with age. The levator arcus-palatini/hyoidei muscles which in *Aldrovandia* (as in *Polypterus*) slant forward and upwards to insert on the frontals, are placed more vertically in *Halosaurus*. The greater interorbital width seems related to the larger surface required for the muscle insertions in *Aldrovandia*. Perhaps, too, the wider spacing of the supraorbital lateral-line canals, concomitant with wider frontals, explains the differences in squamation. Scales are developed in *Halosaurus* in which the canals are close together, but not in *Aldrovandia* in which they are wider apart.

The larva under discussion has developing scales only in the giant suborbital and mandibular canals, so that one cannot rely on this character here. The levator arcus palatini muscles (Text-fig. 5) are placed almost vertically and originate on the posterior border of the orbit and the lateral wall of the cranium. The supraorbital canals, on the other hand, are not very close together, running almost along the upper rims of the orbits. One might perhaps expect a broadening of the head from the compressed state pre-supposed in a leptocephalus head. Also, the origins of the levator arcus palatini muscles are narrow crescents on the frontals of a small syntype of *A. phalacra*, suggesting that the muscle may increase in bulk during

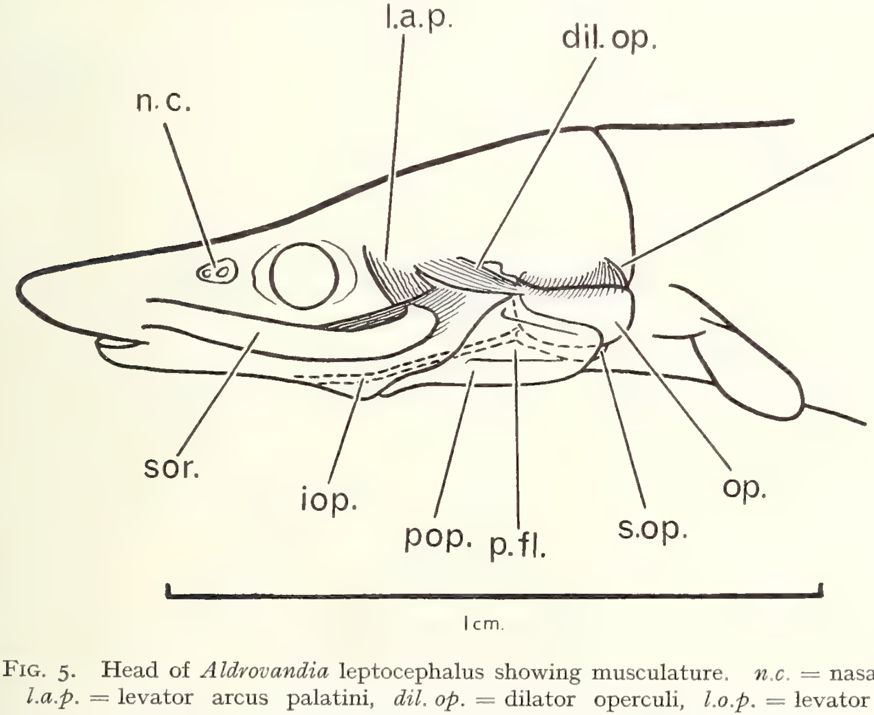

FIG. 5. Head of *Aldrovandia* leptocephalus showing musculature. *n.c.* = nasal capsule, *l.a.p.* = levator arcus palatini, *dil. op.* = dilator operculi, *l.o.p.* = levator operculi, *op.* = operculum, *s.o.p.* = suboperculum, *p.fl.* = preopercular flange, *pop.* = preoperculum, *i. op.* = interoperculum, *sor.* = suborbital lateral line canal.

development. A shift forward of the origin of the muscle from the wall of the brain case to the dermal bones roofing the orbits, may occur at metamorphosis, and presumably at a time when the larva is not feeding. On the basis of criteria currently used to separate genera it is not possible to decide whether the larva is a *Halosaurus* or an *Aldrovandia*. The facts, that the interorbital width is narrow, and that the levator arcus palatini muscle is placed nearly vertically, seem insufficient for assigning it to the genus *Halosaurus*.

The characters used to separate the species of the family Halosauridae, as adults, are largely valueless when applied to a larva in which the body proportions are altering to such an indisputably major extent. This is best emphasized by a comparison of the body proportions assembled in Table II. Measurements for the 7 species of Halosaur examined are set out, using the same material as detailed in Table I. For specimens that had obviously lost the tip of the tail, the length is given, followed by a plus sign. Since many had stood on their snouts in jars for almost a century, their rostra were bent, so that it is impossible to give reliable length data, irrespective of tail-truncation. Standard lengths are given to the nearest millimetre, but should be interpreted with caution. Lastly there is the factor of shrinkage following preservation. In the last century much material was placed in strong spirit, and " hardened ". Johnson (1863) in his description of the holotype of *H. ovenii* quotes the standard length as 18 $\frac{5}{16}$ in. (= 464 mm.). Günther (1887) gives the length of the same specimen as 17$\frac{1}{2}$ in. (= 444 mm.), and my measurement in 1965 showed it to be *c.* 440 mm. Assuming comparable levels of accuracy in measurement, in the first 24 years after its preservation, the type had shrunk by *c.* 20 mm., and shortened by another 4 mm. in the following 78 years. Halosaurs are rather weakly ossified fishes, with more bone in the head region than elsewhere, so the head is probably least subject to shrinkage except in the mucous-filled snout region. Shrinking along the vertebral column, offset by good fixation of the nervous tissue, perhaps explains Vaillant's observation that the spinal-cord in a specimen of *H. johnsonianus* was bent forward in a pleat, beneath the cerebrum (1888 : 182). It is plain that no great reliance can be placed on the proportions given in Table II, but they provide a convenient and uniform series of data for rough comparison. The material has been arranged in order of decreasing standard length, with the larval measurements placed at the bottom, so that allometric phenomena should be more readily apparent for species with adults of comparable size. Three features seem worthy of comment. Firstly the *standard length* : *head-length* ($S_L : H_L$), and the *preventral-length* : *head-length* ($V_L : H_L$) ratios are much higher in the larva, 20 and 3 respectively, than in any of the adults (maxima of 9·8 and 2·6), while the *body-depth* : *head depth* ($B_D : H_D$) shows the same trend (2·1 in the larva, and a maximum of 1·9 in the adults). This is the equivalent to stating that the larva is a *leptocephalus* (= "small head ", in Greek). The larval head is smaller in all dimensions, relative to the body, than in the adults. Secondly the larval *body depth* : *head-depth* ratio is closer to that of the largest, but more than twice the value for the smaller " adults " measured. It seems that the larva becomes more shallow-bodied following metamorphosis, and the adults

TABLE II

Body Proportions a. *Adults*

Species	(S_L) Standard length (mm.)	(H_L) Head length (mm.)	(H_D) Max. head depth (mm.)	(B_D) Max. body depth (mm.)	(V_L) Length from snout to ventrals (mm.)	$S_L : H_L$	$B_D : H_D$	$H_L : H_D$	$V_L : H_L$
A. macrochir	535	58·3	30·5	37·0	142	9·2	1·9	1·2	2·4
A. rostrata	495	53·4	20·5	25·9	128	9·3	1·3	2·6	2·4
A. mediorostris	445+	51·8	23·6	24·3	105	>8·6	1·0	2·2	2·0
H. ovenii	440	45·1	21·2	31·9	120	9·8	1·5	2·1	2·6
A. affinis	420	44·4	16·5	21·5	107	9·6	1·3	2·7	2·4
	410+	47·2	17·6	23·9	116	>8·7	1·3	2·7	2·5
H. johnsonianus	381	41·2	15·6	14·9	91	9·3	0·9	2·6	2·2
	334+	38·9	13·4	13·4	90	>8·6	1·0	2·9	2·3
A. phalacra	207+	28·0	11·6	10·0	66	>7·4	0·9	2·4	2·4

Body Proportions b. *Larva*

Species	(S_L) Standard length (mm.)	(H_L) Head length (mm.)	(H_D) Max. head depth (mm.)	(B_D) Max. body depth (mm.)	(V_L) Length from snout to ventrals (mm.)	$S_L : H_L$	$B_D : H_D$	$H_L : H_D$	$V_L : H_L$
Sp. ?	190	9·5	3·5	7·3	28·5	20·0	2·1	2·7	3·0

become deep-bodied again after the abdomen has been distended by the gonads. Lastly, the *head-length*: *head-depth* (H_L: H_D) ratios seem to show specific differences. The larval ratio appears comparable with the figures for the adults; the precocity of the larval head is noted above. But as the adult snouts have been crumpled to such a varying degree, one can only suggest that these figures make it less likely that the larva is one of the following: *A. machrochir*, *A. mediorostris* or *H. ovenii*.

Returning to Table I, the possible systematic value of the segmentation may be considered briefly. Two prefatory remarks are necessary. There is no absolute correspondence between myotomes and vertebral numbers. The myotomes act across the vertebrae, and the first vertebra counted in the radiographs appeared to be a hemicentrum (the basioccipital, fused to the basisphenoid?). One might expect at least one myotome fewer than the vertebral number in the front trunk-region. Also, the thickness and curvature of the body-wall means that the position of the pectoral girdles and the paired-fin insertions, relative to the vertebral column is subject to some variation dependent upon the angle at which the radiograph was taken, the posture in which the specimen was preserved and the state of contraction of the body musculature. For these reasons a direct comparison between vertebral numbers in the adults and myotomes in the larva, seems unjustified where the differences in segmentation over the range of species examined, is so slight. Secondly it should be noted that the lectotype of *A. macrochir* is that chosen by Günther himself, in his final report on the Challenger fishes (1887). In view of the lack of exact information on the effect of muscular contraction on the position of the fins relative to the vertebrae, the information in Table I may simply be regarded as showing a general conformity of the larval segmentation with that in adult halosaurs, in addition to indicating the magnitude of the anal migration at metamorphosis (see p. 449). Perhaps, though, the rather small number of vertebrae anterior to the ventrals makes it less probable that the larva is either *A. phalacra* or *A. mediorostris*. The data in Table I have been arranged with the "adults" of the different species placed in descending order for the number of preanal segments. It will be seen that for the adults the number of segments anterior to the dorsal and ventral fins decreases in this same order, with the exception that the dorsal fin is further from the head in *A. phalacra*. The present standard lengths in this Table are placed above; below them the first published figures, converted to mm., are given in parentheses. The only characters that really might seem available for both adults and larvae are those of the ray formula. Unfortunately almost nothing is known about the range of intraspecific variation, and in relying on published data which have not been adequately reviewed, one is apt to be engulfed in the quicksands of error amassed unfathomed over a century of time. Assuming all published synonymies to be correct, Table III presents the available data for comparison with the larval fin-ray formula and branchiostegal numbers given above. Certain previously unpublished details could be added thanks to Dr. P. H. Greenwood and Mr. N. B. Marshall who allowed me to see type and other material kept in the British Museum. Such details are shown by an asterisk in the Table. Before looking more closely at the ray formulae it may be remarked that the ray count for the larval pectoral fin given above is probably a conservative figure. The radials and their rays become so small towards the lower border of the fin that they are exceedingly difficult to see.

The species in Table III are arranged in descending order of branchiostegal and fin-ray numbers, except that with *Aldrovandia* the species with a narrow interorbital width (Hawaiian forms, and *A. phalacra*) are placed first, while the species *affinis*, *gracilis* and *rostrata*, which seem to form a natural group, are placed after *A. mediorostris*. Where an author gives an incomplete description of a type specimen, but gives supplementary details for cotypes, such data are given in parentheses. Sizes originally cited in inches have been converted to millimetres. In general only the largest size is given where more than one specimen is treated. Under the head " origin of material " only approximate information is given, as this is often all that is offered by early authors. Full data have been assembled in the Gazetteer (see Appendix). The column " nominal species and genus " shows in brief what changes have occurred in nomenclature. For the sake of brevity and to avoid tedious repetition the full history of transfer from genus to genus is omitted. The next column on the right indicates the author for final recognitions of synonymy and gives additional brief notes where these seem necessary. Where published details are available, all the species of *Halosaurus* have a branchiostegal ray count of 12 or more, whereas in *Aldrovandia* the count is generally smaller, with the exception of Hawaiian forms. Likewise in *Halosaurus* the number of pectoral fin rays tends to be higher, though apparently less markedly so. With respect to the ventral fins the species of both genera have between 7 and 10 rays. The larva has 10 branchiostegal rays (not including the interoperculum) resembling *Aldrovandia*. The remaining ray numbers would fit *A. affinis*, *A. gracilis* or *A. phalacra*. *A. phalacra* has been eliminated on evidence given above, so the larva may probably be referred to as close to the species *A. affinis*. Further than this it seems unwise to venture. As an additional comment one may note as a curiosity that in *Aldrovandia* the enlarged scales of the lateral line are spaced at intervals of roughly 1 to every 3 rows of body scales. The same periodicity was noted above in the distribution of ventral melanophores : 1 about every 3 myotomes, in the larva.

Summarizing the data given above, the larva described is probably a metamorphosing leptocephalus of some species of *Aldrovandia*. Its exact identity will only become clear when more precise accounts of the head morphology of the different halosaurs become available, and when the family has been reviewed. The present tentative determination relies largely on fin-ray and branchiostegal numbers, whose systematic value has not been investigated for this group of fishes.

ON THE RECORD OF A HETEROMOUS LARVA FROM THE INDIAN OCEAN

One may turn at this point to an interesting record published by Mead, 1965 while the present work was in preparation. The title of the paper " The larval form of the Heteromi " is, perhaps, misleading, as the material treated consists of only one larva, stated to be an *Aldrovandia*, and of a juvenile (postmetamorphosis) halosaur. Both specimens were taken in the Indian Ocean. The juvenile specimen

TABLE III

(Explanation : pp. 458-459 of the text)

Genus and species	Branchiostegal rays	Gill rakers (1st arch)	Fin rays				Size (S.L.) (mm.)	Origin of material	Author	Nominal species (and genus)	Synonym given by:
			P.	V.	D.	A.					
Halosaurus Johnson, 1863											
radiatus Garman	21–23	15–17	14	9	11	—	240	Gulf of Panama	Garman, 1899	—	—
	21	16	13	8	10	100	*c.* 125	Peru-Chile trench	Bussing, 1965	—	—
pectoralis McCulloch	18	17	16	10	10 (12)	158	545	Gt. Australian Bight, S. of Eucla	McCulloch, 1926	—	—
güntheri Goode & Bean	—	—	16	10	11	186?	—	W., N. Atlantic	Goode & Bean, 1895	—	—
attenuatus Garman	15	11	15	8	11	—	342	Off the Galapagos Is.	Garman, 1899	—	—
ovenii Johnson	14	16*	11	10	11	191	465	E., N. Atlantic off Madeira	Johnson, 1863	—	—
	15	—	—	10	11	180?	570	E., N. Atlantic	Vaillant, 1888	—	—
	—	—	13	10	11	191	375	S Atlantic off Congo Coast	Poll, 1953	—	—
carinicauda (Alcock)	13	—	15	10	11	—	393	Andaman Sea N. of Cinque Is.	Alcock, 1889	" Halosaurichthys "	Alcock, 1896 : changed to *Halosaurus*
parvipennis Alcock	13	—	12–13	10	9	—	381	Laccadive Sea	Alcock, 1892	Put, together with *carinicauda*, as synonym of *A. mediorostris* : Alcock, 1896 ; opinion revoked Alcock, 1899 ; Norman (1939 : 46) suggests *carinicauda* and *parvipennis* may after all be synonyms.	
	12–13	—	12–13	10	9–10	—	*c.* 394	Laccadive Sea and Arabian Sea off Malabar Coast	Alcock, 1899		
johnsonianus Vaillant	12	—	—	9	11	186	390	East, N. Atlantic	Vaillant, 1888	—	—
	12	—	15	9	10–11	—	408	East, N. Atlantic	Collett, 1896	—	—
	—	16	—	—	9	200?	200 and 363	East, N. Atlantic	Fowler, 1936	—	—
ridgwayi (Fowler)	—	13	12	7	10	140	354	Philippine Islands	Fowler, 1933	" Halosauropsis ". Description ! A scaly head, lateral line scales not enlarged and a narrow interorbital width, are the generic characters of *Halosaurus*.	
										[The case for abandoning " *Halosauropsis* " Collett, 1896 is clear ; and ably put by Barnard (1925 : 167)]	
Aldrovandia Goode & Bean, 1895											
kauaiensis (Gilbert)	13	23	14–15	9	11	—	655	Vicinity of Kauai, Hawaii	Gilbert, 1905	" *Halosauropsis* "	vide supra.
proboscoidea (Gilbert)	(11)	15	14	9	11	—	422	Kaiwai channel, Hawaii	Gilbert, 1905	" *Halosauropsis* "	vide supra.
verticalis (Gilbert)	12	24	14	9	11	—	295	Vicinity of Kauai, Hawaii	Gilbert, 1905	" *Halosauropsis* "	vide supra.
phalacra (Vaillant)	10	(19)*	(13–14)*	8	10	200?	430	E., N. Atlantic	Vaillant, 1888	" *Halosaurus* "	Goode & Bean, 1895
	—	16–18	9	8	11	—	348	" Indian Ocean "	Brauer, 1908	—	—

***Aldrovandia* (contd.)**										
macrochir (Günther)	12	(14)	11–13	10	13	—	545	" Off Gibraltar "	Günther, 1878	(Lectotype chosen by Günther, 1887) " *Halosaurus* " Goode & Bean, 1895.
	12	—	—	9	12	200?	600	E., N. Atlantic	Vaillant, 1888	— —
	12	—	11–13	9–10	11–13	190–200?	615	E., N. Atlantic	Collett, 1896	— —
	12	—	—	9	11–12	—	—	W., N. Atlantic	Gill, 1881	" *goodei* " Günther, 1887.
	12	—	—	9	12	—	c. 608	Off Cape Pt. E., S. Atlantic	Gilchrist, 1906	" *niger* " Barnard, 1925.
	—	—	—	9–10	12–13	—	650	Cape Pt. and Table Bay, S. Africa	Barnard, 1925	— —
mediorostris (Günther)	11	17*	8	8	11	—	444	W. of Philippines	Günther, 1887	" *Halosaurus* " Goode & Bean, 1895.
	11	—	8	9	11	—	—	Indian Ocean, E. of Maldives	Alcock, 1899	— —
	11	—	8	9	11	—	285	Bali Sea	Weber & de Beaufort, 1922	— —
affinis (Günther)	10*	13–14*	11–13*	9–10*	10*	—	421	" Japan "	Günther, 1877	" *Halosaurus* " Goode & Bean, 1895. Alcock, 1896—synonym of *A. mediorostris*—revoked in Alcock, 1899.
	12	14	12	9	12	—	—	Gulf of Manaar (off Ceylon)	Alcock, 1889	" *anguilliformis* " Barnard, 1925.
	10	8	13	9	11	c. 175	533	Laccadives, W. of Mangalore. " Arabian Sea "	Alcock, 1890	" *hoskynii* " Goode & Bean (1895 : 130) : probably = *affinis* Alcock, 1899 given as = " *anguilliformis* ".
	11	—	13	9	11–12	c. 200	482	Laccadives, W. of Mangalore. " Arabian Sea "	Alcock, 1890	— —
	12	21–22*	9	8	12	—	190	Indian Ocean off Maldives	Alcock, 1898	" *nigerrimus* " Weber (1913 : 93) ; tentative synonymy (see note p. 462, of the present paper).
	10	—	9–10	8	10–11	—	330	Timor Sea	Weber, 1913	— —
	—	—	—	9	12	—	—	Off Cape Point E., S. Atlantic	Gilchrist, 1906	— —
	—	—	—	9	12	—	525	Cape Pt. and Table Bay, S. Africa	Barnard, 1925	— —
	—	15	13	9	11	c. 166	600	Gulf of Mexico	Goode & Bean, 1895	" *pallida* " Mead, Bertelsen & Cohen (1964 : 583).
	—	14	12–14	—	—	—	512	Gulf of Mexico	Grey, 1958	as " *pallida* " —
gracilis Goode & Beane	10	14	—	—	—	—	490	Gulf of Mexico and Caribbean Sea	Goode & Bean, 1895	— —
	—	15	10–11	—	—	—	536	Gulf of Mexico	Grey, 1958	— —
rostrata (Günther)	9	c. 12*	10*	9–10	10	—	507	" Mid Atlantic "	Günther, 1878	" *Halosaurus* " Goode & Bean, 1895. Günther, 1878 notes the great similarity w. *A. affinis* (p. 242). Regan (in Gilchrist, 1906) suggests they may be identical. Barnard, 1925 notes differences in scale nos. along the lateral line.
Larva	10	9	10	8	0	0	190	E., N. Atlantic " off Madeira "	—	— —

was tenatively identified as "*Halosaurus nigerrimus*". The latter was synonymized by Weber (1913) with *Aldrovandia affinis* (see Table III), but Dr. S. McDowell (in litt.) suggests an alternative synonymy with *A. phalacra*. This agrees with the fact that Dr. A. G. K. Menon who examined the specimen of *H. nigerrimus* finds a much higher number of gill rakers than in *A. affinis* (see Table III). Thus on first appearance, the material would consist of two specimens (only one a larva), of a single genus of halosaurs, i.e. *Aldrovandia*. No evidence whatsoever is presented concerning the type of larva that either the lipogenyids or the notacanths possess.

The larva is offered as being a leptocephalus, though apart from the comment that it bears a general resemblance to a larval eel, no mention is made of what specifically leptocephalus characters it has. Concerning its ordinal determination, one may remark that the specimen does not appear to possess pelvic fins, which all Heteromi do. Further, the drawings made for Mead show the nasal capsule with one aperture—halosaurs, notacanths, and lipogenyids have two nasal openings. An interesting observation by Mead is that his larva appears to have luminous organs. These organs are probably not present in any of the Heteromi—Brauer, 1908 (p. 119) considers that luminous organs reported by some early observers (e.g. Günther), are in fact only neuromast cushions. The only character given for assigning the specimen to the genus *Aldrovandia* is an obscure reference to jaw characters said to be generically specific. As these have not been used by previous authors, it must be hoped that this point may be clarified when McDowell's revision of the Heteromi (viz. Marshall, 1962 : 261), finally appears in the Sears Foundation series *The Fishes of the Western North Atlantic*. Until then it is not possible to give a proper assessment of this point. In view of the fact that none of the opercular characters typical of halosaurs were found, and that no giant lateral line canals were shown to be present, the statement that the head structure was unmistakably that of a halosaur (Mead, p. 1) thus comes as a surprise. An incomplete ray formula is given, and since details of segmentation are obscured in the available figure by the stipple-shading, there appear to be no reliable characters from which one might settle the identity of Mead's larva. It therefore seems wisest to reject the record, for the present, as representing a heteromous larva. Should it ultimately prove to be that of a halosaur, it would be of great interest, as when fresh it was transparent, and it is a larva with at least one enlarged tooth[1] (cf. p. 449 above). Further discussion must however, be waived, until a better description becomes available, and the identity of the material is properly established.

METAMORPHOSIS IN THE HALOSAURIDAE

After the brief review given above comparing adult characters with those in the larva from Madeira, one may return to the process of metamorphosis. It is not possible on the basis of a single specimen to give a full account of this transition

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[1] *Since writing this Dr. Mead has kindly allowed me to see the specimen. It is larger than the halosaur leptocephalus described above, and is badly damaged. This is perhaps to be expected of material from an Isaacs-Kidd tow of nearly twelve hours! Many specimens from hauls lasting two hours are almost unrecognizable. I would suggest that the transparency of the specimen when fresh was due to the almost complete loss of (probably dark black) skin. I was unable to find any enlarged teeth. Other details might have been seen had clearing and dissection been carried out.*

in the Halosauridae, but additional information may be sought from two other specimens recorded in the literature. These further specimens are Alcock's "*H. nigerrimus*" (1898) of 190 mm. from 905 m. off the Maldives, and Gilchrist's (1908) 120 mm. specimen from North of Cape Point, South Africa, which he provisionally assigned to "*H. niger*". The former was tentatively referred to *A. affinis* by Weber (1913), the latter, in like fashion, to *A. macrochir* by Barnard (1925), (see Table III). Alcock's specimen is apparently an *Aldrovandia* as in his catalogue (1899) he says that there are about 30 much enlarged lateral line scales between the gill opening and the vent. As there are upwards of 60 myotomes anterior to the vent (Table I), this implies 1 lateral line scale per 2 myotome segments and referring back the comment on the usual frequency of lateral line scales (p. 459) suggests that Alcock's "about 30" should be treated with caution.

The forward shift of the anus and renal pore at metamorphosis has been discussed (p. 449, and Table I), as has the proportional increase in the size of the head relative to the body (p. 456, and Table II). Further, the body changes from its laterally compressed ribbon-like leptocephalus shape, to the cylindrical body typical of the adults. The pigmentation of the leptocephalus is confined almost completely to the ventral series of dark spots. Gilchrist's 120 mm. specimen had a black head, and a white body. It seems quite possible that in halosaurs generally, the head darkens before the rest of the body, in contrast to *Anguilla* where the pigmentation spreads forward from the tail, though the ease with which halosaurs seem to lose body skin must be remembered. Alcock's specimen of 190 mm. is described as being uniformly jet black. The small size of both these juvenile halosaurs, and the relatively large size (190 mm.) of the only known leptocephalus, tempts one to wonder whether initially these fishes "grow by shrinking" such as Hollister (1936) has shown to occur in *Albula*. As however, the identity of all three halosaurs concerned is uncertain, since the different species of *Aldrovandia* appear to vary greatly in adult size, and because of the possibility that as in eels (Bellini, 1907, etc.), so in halosarus, small leptocephali may give rise to males and large leptocephali to females, the matter can only be decided when much more material of the young stages becomes available.

Even more striking are the changes in the arrangement of the fins. Consideration of the dorsal and anal fins in the discussion of the adult ray formula above, was omitted. The larva had no anal, and the larval dorsal is merely a long dorsal fold. The changes at metamorphosis are thus considerable in this respect. An adult dorsal fin with a short base and from 10–12 rays (see Table III) appears in front of the larval fin fold. The fold may disappear comparatively late in development in *Aldrovandia*—Alcock's 190 mm. "*H. nigerrimus*" retains a low fold of skin which begins at an enlarged scale two-thirds of a head length behind the dorsal fin and is not continued to the end of the tail—or, in *Halosaurus*, may be retained in the adult. The 394 mm. holotype of *Halosaurus carinicanda* Alcock, 1889 is described as having "a low median fold of skin, (not much more than half a millimetre high) . . . enclosing distant, thin, sharp, irregular indurations", (auct. cit., p. 455). The *Aldrovandia* larva described here did not appear to have "indurations" in the fin fold ; this may be a character to be expected in larval *Halosaurus*. From

Alcock's data it seems likely that the larval fin fold is resorbed from the tail end first. After the anus had shifted forward, a long anal fin must develop. No signs of an anal fin could be seen in the present leptocephalus (the tip of the tail was damaged), but in the adults the anal occupies 156–256 segments in *Aldrovandia* (198–201 in *Halosaurus*), on the basis of evidence presented in Table I. Further changes in the fins appear to include an alteration in the " set " of the pectorals ; they are set rather high in the adults, and low in the larva. The change seems concomitant with the development of the swimbladder (cf. Harris, 1937), of which no sign could be detected in the larva. In eels the swimbladder first appears in the elvers.

It is hard to guess at what time the body scales appear in halosaurs. In eels they appear long after metamorphosis has been completed ; 2–4 years later in *Anguilla*, where they first form along the lateral line and in the mid trunk-region (Hornyold, 1937). Alcock (1899), describes his 190 mm. specimen as having scales " on the temples and cheeks ". Those of the lateral line he notes as adherent, the other scales he dismisses as " deciduous ", which might have meant that they had not yet developed were it not for a figure published by Alcock, and Dr. Menon's assurance that body scales are indeed still present. It may still indicate the development of the body lateral-line scales before the others, and in this case the sequence of the appearance of scales would resemble the pattern in *Anguilla*.

Finally there are some metamorphic changes in the arrangement of muscle and bone. In the body the muscles thicken and fold forward at their dorsal and ventral ends so that the myotomes lose their simple V-shape noted in the larva. At the same time the ribs and 2 sets of intermuscular bones (see Plate 1) develop, the space between the larval myotomes disappears as the jelly-filling is resorbed (see p. 449), and the muscles meet ventrally below the viscera as these move up to their definitive position closer to the vertebral column which forms along the notochord. In the head, changes appear to involve the opercular bones, teeth, the dermal roofing of the skull and the musculature of the mandibular-plate. The interoperculum broadens from the narrow branchiostegal-like splint of the larva, to give the paddle-shaped bone seen in the adults. It is likely that a set of larval teeth is shed before the development of the granular adultiform dentition. The present specimen had no teeth, so presumably had already lost its larval set. It is suggested above (p. 456), that the levator arcus palatini muscles shift their insertion at metamorphosis. Dramatic changes including the fusion, degeneration, and the alteration of insertions and origins of various muscles are known to occur in amphibian metamorphosis (Nieuwkoop & Faber, 1956 : 100), which makes it seem probable that analogous changes could occur in fishes. It is also suggested here that the frontals may broaden in *Aldrovandia*, though whether this happens at metamorphosis or after it seems uncertain. Of the smallest known halosaurs all appear to have a narrow interorbital width, and three at least (the Madeira larva, " *H. nigerrimus* " and Weber's (1913) " *H. carinicauda* " of 280 mm.), have long median dorsal fin folds. It seems distinctly possible that a narrow interorbital width in *Aldrovandia*, and a dorsal fin fold in *Halosaurus* may occur as larval features retained in some adults by that process commonly called neoteny.

FOOD, FEEDING AND CLASSIFICATORY FEATURES IN HETEROMOUS FISHES

In a broader setting, the discovery of a metamorphosing halosaur leptocephalus makes clearer the ties between the Apodes and " the Lyopomi " (Berg's Halosauriformes), but what of the notacanths? The latter share many osteological peculiarities in common with the halosaurs. Likewise the notacanths have an eel-like swimbladder (Marshall, 1962). There seem good grounds for believing that notacanths eels and halosaurs derive from a common stock, and all 3 may be regarded as members of a natural group of eel-like fishes. The bone structure of eels perhaps serves to isolate them somewhat from notacanths and halosaurs. A third family of heteromous fishes, the Lipogenyidae, is omitted from the following discussion : the author can add no new information on its status.

The major differences between notacanths and halosaurs lie in the structure of the lateral-line canal-system and the operculum. As Marshall (1962) has shown the intergradation between spines and soft rays in the notacanths, and there are frequent references in the literature to spines in halosaurs, the justification disappears for separating the notacanths as spiny fishes from the halosaurs as soft-finned. Gosline (1961 : 36) states that the pelvic structure of notacanths is unique. This is not clear from his previous discussion in the same paper (pp. 17–21). If based on the " pungent " elements in notacanths, it should be borne in mind that halosaurs are also reported as possessing pelvic spines by many authors. Halosaurs have lateralis canals lying external to the scales and the opercular apparatus (cf. Günther, 1887 : 238–239 : " luminous organs ") and have large free branchiostegal folds. Notacanths have a larger ,operculum, suboperculum and interoperculum, and the preoperculum small, while the lateral line canals lie internal to the scales, both on the head and the body. These are considerable differences, but one may ask how far they are related to functional requirements.

Baglioni (1907) divided marine fishes into four main groups according to their habits and noticed accompanying differences, chiefly in the branchiostegal apparatus, when considering respiratory mechanisms. Bottom living fishes tend to have a large branchiostegal apparatus, while in pelagic fishes the opercular apparatus is large and the branchiostegal flap small. These differences parallel those between notacanths and halosaurs. The following is offered as a possible interpretation, considering the differences in relation to feeding requirements in the two groups.

Actively swimming pelagic fishes pursue their prey, and whether or not they catch it may be thought of as depending largely " on who swims fastest ". Assuming this is the predator, all that is required is for it to open its mouth at the right moment, when, if the victim is of a suitable size, it will pass down the gullet of the oncoming pursuer. Water can flow over the gills automatically during swimming, and no extra pumping is needed. For a bottom living fish the situation is different. An excess of guile over muscle may be advantageous, but of no less importance is the possession of a large branchiostegal flap. Potential food animals crawling over the bottom may disappear into places not accessible to the predator. A rapid gulp, involving a sudden intake of water through the mouth, is thus important, and is one function of a well developed flexible branchiostegal flap. The fold can be fanned forwards and down by the hyohyoid muscles in the web between the rays, so that the extrabranchial cavity expands. A flick of the web, produced by relaxation of the muscles joining the tips of the rays, and by a rotation of the hyoid bar by muscle joining it to the mandible, suddenly pushes back water from outside and behind the gill cavity resulting in an inrush of water through the rictus as the mouth-floor sinks. The development of the branchiostegal flap may therefore be important as part of a complex mechanism, [also involving the mouth, the shoulder girdle and the operculum (Tchernavin, 1953)], for the purpose of catching moving prey, in addition to the need for pumping water over the gills (Hughes, loc. cit.). Where the opercular fold is supported chiefly by the branchiostegal rays a highly flexible and much more readily expansible structure is achieved than when the opercular bones are larger and the branchiostegal flap smaller.

Both halosaurs and notacanths are benthic fishes, but whereas notacanths can browse at leisure on banks of sessile sea anemones, the halosaurs appear to feed almost exlusively on benthic microcrustacea. Notacanth stomachs are packed with fragments of actinians (Tucker & Jones, 1951 ; Wheeler, personal communication). Records of food from halosaur stomachs have suggested that they were catholic feeders. Collett (1896 : 151) records 2 *Rossia* of 28 mm. from the stomach of one *A. macrochir* ; mud, sand, foraminifera, sponge spicules and a *Cleodora* shell from the intestine of another. The *Rossia* were described as " well preserved " and may have been swallowed in the trawl-bag as it was hauled in by the yacht Hirondelle. Günther (1887 : 233) records " shrimp-like crustaceans " from the stomach of a third *A. macrochir* apparently from the Marion Islands, while Bell (1887) describes a trematode parasite from the ureter of a halosaur and gives the provenance of the material as " off Cape St. Vincent . . . 1,090 fths. ", (= 1,993 m.). This seems to be an error, as only one halosaur was taken by the Challenger at Station V, off Cape St. Vincent, and this was Günther's lectotype of *A. macrochir*, which shows no signs of having been dissected. Bell's apparent mistake has been reproduced elsewhere (Manter, 1934 : 262 ; Dogiel, 1964 : 285). Günther more probably dissected one of the 4 *A. macrochir* from the Marion Islands (taken at Stn. 146—1,365 fths. = 2,515 m.) prior to its preparation as a skeleton! Mr. Prudhoe, who has kindly examined the material of " *Distomum halosauri* ", Bell, kept in the British Museum, suggests that it may be a *Phyllodistomum*, and in this genus those species whose life history is known (species from freshwater fishes etc.) always have a larval stage whose host is a lamellibranch. This parasite record thus suggests that *A. macrochir* may also feed on bivalve molluscs. It is likely that the sloping levator-arcus-palatini muscles in *Aldrovandia* help rock the palatoquadrate back and forth, and a grinding mechanism of this type would seem well suited to triturating lamellibranchs. Zugmayer (1911) records crustaceans and sand from the stomach of another *A. macrochir*. An *Aldrovandia* among material collected by the Rosaura expedition from the Atlantic had its stomach packed with fragments of Cumacea, tanaids etc. recalling Günther's " shrimp-like crustacea ". A remarkable number of recognisably crustacean fragments could also be seen in the radiographs of a series of halosaurs. An astonishingly clear image of a whole tanaid is shown in the hind gut of the type specimen of *A. rostrata* (Plate 1). This evidence suggests that crustacea form, at least, the basis of the halosaurs' diet. The Tanaidacea live in tubes which they spin for themselves. While the Cumacea are highly active little crustaceans which swim for short distances, then burrow back rapidly into the silt in which they live. The great development of the sense organs of the lateral line, and the large contribution to the support of the opercular fold by the branchiostegal rays, may thus be features connected in halosaurs with catching moving prey, and the chief differences (vide supra) between the two groups of heteromous fishes would then resolve themselves as functional devices related to their markedly divergent food requirements. A possible difference remains in the mode of development. Whether or not notacanths have a leptocephalus larva, remains an unanswered question. N. B. Marshall (pers. comm.) has found in the British Museum collections a 115 mm. notacanth from Messina which is laterally flattened and is perhaps a young post-larva. Earlier stages remain unknown.

REPRODUCTION IN HALOSAURS AND OTHER FISHES WITH LEPTOCEPHALUS LARVAE

A prolonged period of development implies a small number of generations over a long time-span, hence provides less material for genetic variation or natural selection to act upon than would be so were development and maturation more rapid, given in both cases a similar level of fecundity. It is thus not surprising to find in the groups of fishes with slow developing leptocephalus larvae a range of morphological oddities otherwise associated with extinct or ancient forms. (The gular plate of *Elops*, the rostral commisures of *Pterothrissus*, Elopidae, Megalopidae, *Albula* and halosaurs, the valved conus arteriosus also in *Albula* and *Megalopidae* and perhaps the extra gill bars in *Saccopharynx*, may serve as examples). The simple myotomes of the larva resemble those of the *Acrania*, and perhaps too the anomalous Silurian fossil *Jamoytius kerwoodi* White (1946), in which Ritchie (1960) shows that the V-shaped smears are probably scales. (Presumably they nonetheless correspond to the underlying myotomes). Nor is it strange that fossil halosaurs, very like the living forms, are known from the Cretaceous. Balancing the long life-span, it appears that in those fishes with leptocephalus larvae, for which data are available, prodigious numbers of eggs are produced. Thus estimates of the egg numbers in *Anguilla anguilla* vary between 20 millions (quoted without reference in Bigelow & Schroeder, 1953) and 5–10 millions (Bertin, 1956 : 77), while J. T. Nichols counted 12,201,94 eggs from a 142 lb. *Tarpon atlanticus* (cited by S. F. Hildebrand, 1963 : 115). This must allow a maximum of genetic recombination at meiosis, for gametes from a single parent, but the effect will be enhanced if, as in *Anguilla*, the adults congregate to spawn, since then the recombination possible in the zyogote may be as between a larger number of adults assuming that the freely shed eggs of any female may be fertilized by sperm from a number of different males. This may explain how the eels which congregate to spawn have acquired many striking adaptive modifications of basic teleost body form in the adult in spite of their longevity, whereas *Tarpon* which probably spawns in pairs, retains many " primitive " unmodified characters, in addition to a few advanced ones such as its secondary lung-like swim bladder. Acting against the variation to be expected from such enormous fecundity, is the length of vulnerable larval life. Only a very few of the immense numbers of leptocephali produced will survive to adulthood. Indeed the sunfishes find leptocephali sufficiently palatable to feed solely upon them when opportunity allows, preferring them to their more usual diet of jellyfishes. Grassi (1896 : 263) found sunfishes with their stomachs packed with eel-leptocephali in the Straits of Messina. The low " survivorship " and slow rate of development are probably the two most important factors producing the assortment of " advanced " and " primitive " characters in the fishes with leptocephalous larvae. Now these fishes seem in the main to be of sedentary habit. Gosline (1959), for instance, considers that the chief characters of eels are related to their living in crevices. Halosaurs are benthic, gulper eels are probably not powerful swimmers. The whole complex appears to have renounced higher rates of evolution, and acquired instead, pelagic larvae that act largely as a distributive phase in the life cycle. It is remarkable how widespread many of the fishes with leptocephalus larvae are.

What little information is available on breeding in halosaurs is scattered through the literature. It seems worth summarizing it briefly. All the records of halosaurs fall between the latitudes of 40° North and South of the equator, except for Günther's record of *A. macrochir* from the Prince Edward Islands (Marion Islands), reports of *H. güntheri* and *A. gracilis* from the North West Atlantic where the Gulf Stream carries northward water masses of more southerly characteristics, and a specimen of *A. macrochir* from off Ireland, (see Map, Text fig 6). Within these boundaries of latitude, the halosaurs are world-wide. The depth range for the group appears to be between a record maximum of 5029 m. (= 2750 fths.) for an *A. rostrata* (N. Atlantic), and a record minimum of 383 m. for an *A. affinis* (Timor Sea). The author is not aware of records of halosaurs in nets fished at shallower levels. Most of these fishes were not found in hauls taken above 900 m. or below 3,000 m. and are distributed around the lower edges of the continental shelves and along oceanic ridges. Bathyscaphe observations and deep-sea photographs show that halosaurs normally swim just above the bottom (e.g. Pérès l.c., Marshall & Bourne, 1965). There are records of more than twenty-four halosaurs with eggs. At least five of these females can be referred to the genus *Halosaurus*, and some nineteen to *Aldrovandia*. In *Halosaurus* Johnson's 465 mm. genotype of *H. ovenii* 1863, collected in February had eggs, some of which measure 1·0 mm. in diameter after more than a century in spirit. The specimen came from off Madeira, i.e. at a latitude of c. 32° N. Poll (1953) records a 375 mm. specimen of the same species taken on October 14th, 1948 at 5° 39′ S., which also had ripe eggs, whereas Vaillant, 1888 whose samples covered the period from June to August records that all the females of *H. ovenii* taken by the Talisman had small eggs. A specimen of *H. johnsonianus*, taken on 18th August, 1888 is reported by Collett as having eggs at different stages of development. In some other fishes this condition is indicative of a prolonged spawning period. The

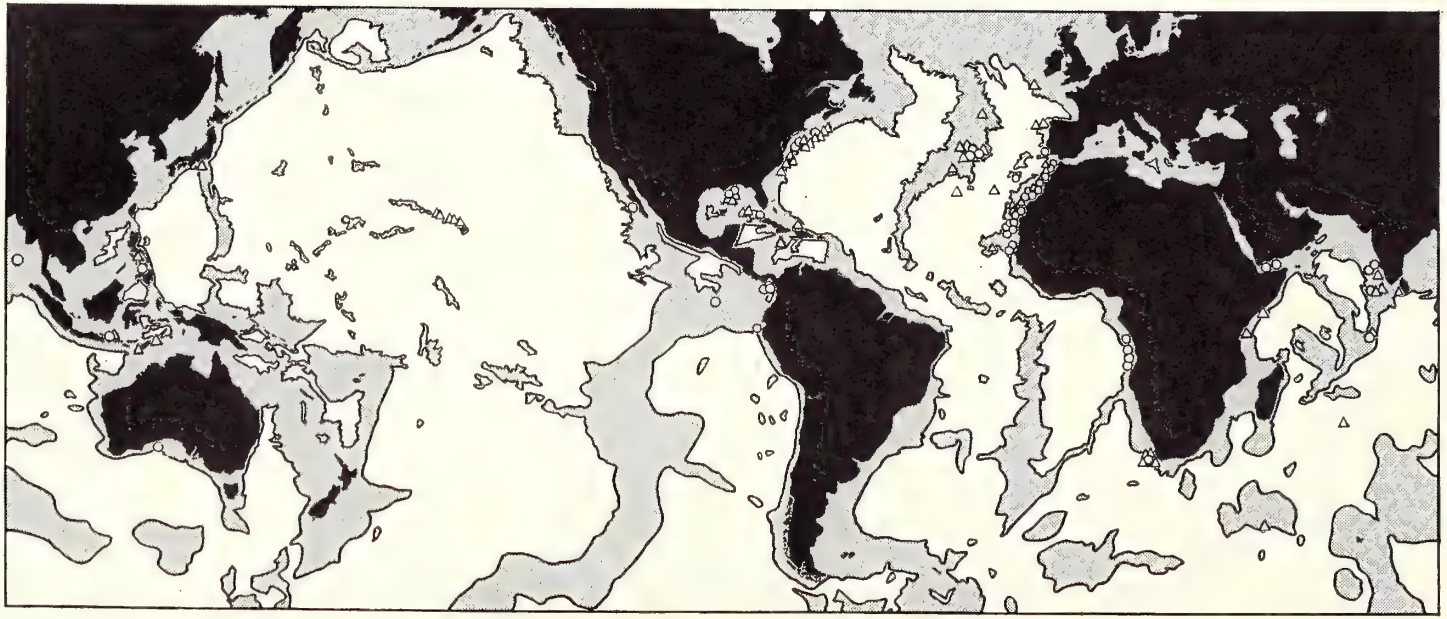

FIG. 6. Map showing the distribution of halosaurs from published records. Land shown in black. The stippled area indicates water of a depth of 2,000 fathoms (= 3658 m.) or less. Circles indicate records of *Halosaurus* species, triangles show records of members of the genus *Aldrovandia*.

picture for the Indian Ocean and the Pacific is similar. A gravid female of *H. parvipennis* was taken by the Investigator at Station 122 on October 21st, 1891, while in the Pacific, an *H. radiatus* with well developed eggs was taken by the Albatross expedition in February, or March of 1891. Poll's record is the only one for the southern hemisphere (see Gazetteer). Records of females with ripe eggs in the Northern hemisphere are thus grouped in the period October to March.

Turning to the genus *Aldrovandia* one finds there are no records at all of females with ripe eggs. Two authors apparently report material of *A. affinis*: Alcock, (1889) says that his two " *H. anguilliformis* " collected on May 5th, 1886 had eggs, and Grey (1958) tells us that twelve of her " *A. pallida* " had tiny eggs when collected on May 26th, 1955. Collett, 1896 had two *A. macrochir*, with unripe eggs, the largest of which were 0·5 mm. in diameter, collected on 31st July/1st August, 1888, and Zugmayer, (1911) examined two specimens collected on 18th August, 1910, one he describes as possessing eggs that were not at all ripe, the other bore eggs considered as not fully ripe. The same author describes an *A. phalacra* collected on the last mentioned date: it has half-ripe ovaries.

In contrast to the genus *Halosaurus*, species of the genus *Aldrovandia* mostly live at greater depths, lower temperatures and higher pressures. Thus on the map, the triangles symbolizing records for this genus, fall in a belt closer to the deep ocean basins, while the circles indicating *Halosaurus* records, are almost all close to the continents. *Aldrovandia* has some very widely distributed species, for example, *A. macrochir* and *A. phalacra* (Atlantic and Indian oceans), and *A. affinis* (all oceans), whereas there are different species of *Halosaurus* for each ocean, and these are often of limited known distribution. The most widely dispersed *Halosaurus* appears to be *H. ovenii* known from both sides of the North Atlantic, and reported from points reaching from Morocco to Cape Town.

There seem then to be differences in the reproductive biology within the family *Halosauridae*. Either the species of *Aldrovandia* have very much smaller eggs, or they migrate to particular spawning-grounds, where they have not yet been caught. Possibly, too, if the eggs of *Halosaurus* species are indeed larger, their mode of development is different. It may ultimately prove no coincidence that leptocephali of *Aldrovandia* are those first known for the family. In any case one may expect a shorter larval life span for *Halosaurus* species on the grounds of their more limited distribution. The data available suggest that female halosaurs mature early in life. Thus Alcock's type of *Halosaurus parvipennis* was 381 mm. long, while Garman's *H. radiatus* was only 356 mm. S.L. An example for *Aldrovandia* is given by Alcocks " *H. anguilliformis* " (= *A. affinis* see Table III) which were ovigerous at *c*. 356 mm. S.L. (this is not a precise length: both specimens were brought aboard in fragments). It seems justifiable to compare the eggs of the genus *Halosaurus*, at least, with those of other fishes. Presuming that the eggs swell after oviposition and the formation of the perivitelline fluid they might be expected to be comparable in size to the pelagic eggs of eels, where diameters of 2·40 to 2·70 mm. are recorded by Schmidt (1930) for *Nessorhamphus*, and 3·3 mm. for an unidentified eel by Beebe (1936). The present record of a larva from 1,110 m.

(bottom at *c.* 3,000 m.) suggests that oviposition may be followed by a larval existence within the horizontal plane inhabited by the adults.

If distribution is associated with length of larval life in fishes not otherwise thought to be powerful swimmers or of migratory habit, perhaps the almost ubiquitous occurrence of the notacanths may be taken as weak circumstantial evidence that they, too, have leptocephalus larvae. Be that as it may, the discovery of a metamorphosing halosaur larva adds another tessera to the mosaic showing the lower teleosts, as a diverse group that has at the same time frequently retained a basic similarity in the pattern of development from egg to adult.

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SUMMARY

1. A single specimen of a halosaur leptocephalus is described, and its characters compared with those of the leptocephali of other fishes.

2. The distinctive features of the specimen are compared with details observable in adult halosaurs.

3. A review is made of such systematic characters in the adults as can be observed in the leptocephalus. Notes of previously unpublished details based on a re-examination of type material are given. It is concluded that the leptocephalus is an *Aldrovandia*, close to *A. affinis*.

4. An attempt is made to outline the processes occurring at metamorphosis.

5. The feeding of adult Heteromi is considered in relation to their systematic status.

6. The reproductive biology and distribution of the halosaurs is discussed.

7. An effort has been made to gather together as full a series of data as possible, relating to published records of halosaurs. These are given in the form of a gazetteer.

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APPENDIX

A GAZETTEER TO HALOSAUR RECORDS

In order to summarize the fragmentary information on the reproductive biology of the Halosauridae it was found desirable to gather together as full a series of data as possible from published records. The immense labour of piecing together these results from station lists, hydrographic papers, studies on bottom deposits, annual reports and charts, leads to the conclusion that it would be valuable to print what has been gathered in this way, if only to save others from this onerous task in the future. Considerations of space preclude the listing of all the papers consulted for this part of the work. A selection of the most important works is given above after the main body of references. Special notice should however be given to the following points. As Eschmeyer (1965) has shown, many of the stations assigned to Blake material by Goode & Bean (1895) and printed in roman numerals in " Oceanic Ichthyology ", are in fact erroneous. Probably the same applies to specimens from " Albatross " stations. It has not been possible at present to trace all such errors. In general the roman numerals have simply been sought against the equivalent arabic numbers given in the lists of Smith (1899). An additional record of *A. macrochir* which does not appear in Goode & Bean, has been added from Tanner's (1886) report on the work of the " Albatross ". Gill's records of " *Halosaurus goodei* " have been combined with Goode & Bean's data for *A. macrochir* : Gill states how many specimens he saw, Goode & Bean do not. This means that the numbers of *macrochir* for the stations concerned are minimal figures, as in some cases specimens formerly separated into the supposedly different forms *macrochir* and " *goodei* ", occurred together, but only Gill's data for numbers of " *goodei* " are available. It should be noted that the Talisman station-numbers given by the biologists concerned with working up the material from the 1883 expedition, are printed in roman type, and include secondary substations. The numbering given by the hydrographers (Parfait, 1884) is, on the other hand, in a simple continuous series of arabic numerals. Caution is therefore necessary in tracing data when referring to the hydrographic lists, from a series of biological records. In spite of the agreement at the Washington meridian conference in 1884 to quote longitudes from Greenwich, the publications on this expedition, even though they appeared some years later than this date, still quote longitude from Paris. Smith gives correct longitude data for both conventions in most (not all) instances, but follows the French hydrographers in printing simplified station numbers which thus differ from those given in Vaillant's (1888) account of the fishes. The early reports on the expeditions of Prince Albert I of Monaco, also quote station-position longitudes from Paris, but corrected data quoted from Greenwich are to be found in Richard (1934). It will be seen that the species occur in the tables in the order of their first discovery in the relevant ocean, with data for species of *Aldrovandia* following records for the genus *Halosauras*. Finally, the asterisks against some bottom temperatures given in parentheses indicate information cited from a different, but closely adjacent station, of comparable depth.

KEY TO ABBREVIATIONS

r.	red
br.	brown
ye.	yellow
gn.	green
ol.	olive
blu.	blue
gy.	grey
bl.	black
wh.	white
-sh.	ish
spkd.	speckled
lt.	light
dk.	dark
rks.	rocks
sts.	stones
sha.	shale
shr. deb.	shore debris
shs.	shells
cor. s.	coral sand
vol. s.	volcanic sand
s.	sand
cl.	clay
m.	mud
for	foraminifera
glob. oz.	globigerina ooze
oz.	ooze
r	radiolaria
bar. nods.	barytes nodules
mang.	manganese
bm.	bottom
hd.	hard
shay.	shaley
bkn.	broken
shlly.	shelly
cs.	coarse
th.	thick
sy.	sandy
my.	muddy
sft.	soft
fn.	fine
reg.	region
w.	with

A Gazetteer to Halosaur Records

Atlantic Ocean

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom temp.	Number of Halosaurs taken
1. *Halosaurus ovenii*							
Johnson, 1863	—	Off Madeira	Feb.	—	—	—	1 ♀ (± ripe)
Vaillant, 1888	Talisman XIX	33° 42′ N., 8° 01′ W.	14.vi.1883	920	ye. m.	10° C.	1
	XXXIII[2]	32° 31′ N., 9° 48′ W.	17.vi.1883	834	r.-sh. m.	11° C.	3
	XLV	29° 08′ N., 12° 26′ W.	26.vi.1883	1,235	sft. ye. m.	8·5° C.	1
	L	28° 35′ N., 13° 10′ W.	27.vi.1883	975	ye. m.	7·2° C.	4
	LII	28° 33′ N., 13° 19′ W.	27.vi.1883	946	s. spkd. bl.	—	1
	LXXII	25° 39′ N., 16° 02′ W.	9.vii.1883	882	my. s.	—	2
	LXXXII	23° 00′ N., 17° 30′ W.	12.vii.1883	932	gn. my. s.	7·0° C.	1
	LXXXIV	22° 54′ N., 17° 26′ W.	12·vii·1883	860	gn. my. s.	7·5° C.	1
	LXXXV	22° 52′ N., 17° 23′ W.	12.vii.1883	830	gn. my. s.	7·5° C.	1
	LXXXVII	22° 03′ N., 17° 33′ W.	13.vii.1883	1,113	gn. my. s.	7·0° C.	20
	XCIII	20° 44′ N., 18° 07′ W.	14.vii.1883	1,495	gn.-sh. my. s.	4·5° C.	1
	XCV	20° 38′ N., 18° 19′ W.	14.vii.1883	1,230	gn. my. s.	—	10
	XCIX	17° 12′ N., 17° 07′ W.	17.vii.1883	1,617	shay. cl.	—	1
	C	17° 16′ N., 16° 59′ W.	17.vii.1883	1,550	gn.-sh. m.	—	1
	CXXVII	38° 38′ N., 28° 21′ W.	15.viii.1883	1,257	gy. m.	11·5° C.	1
Good & Beane, 1895	Blake Ag. 67	Off Havana	1878	439	—	—	—
	Ag. 68	Off Havana	1878	838	—	—	—
	Albatros 2181	39° 29′ N., 71° 46′ W.	23·vii·1884	1,267	gy. m., fn. s.	3·8° C.	2
Gilchrist & von Bonde, 1924	Pickle 517	33° 35′ S., 17° 00′ E.	8·xi·1921	1,097	—	—	10
Poll, 1953	Noordende III 45	5° 39′ S., 11° 25′ E.	14·x·1948	470	br. sy. m.	7·8° C.	1 ♀ (ripe)
	88	10° 45′ S., 13° 07′ E.	12·xii·1948	500	gn. sy. m.	—	1
	97	11° 53′ S., 13° 20′ E.	18·xii·1948	510	gn. m.	8·0° C.	1
	125	8° 28′ S., 12° 45′ E.	7.ii.1948	500	sy. m.	7·28° C.	1
Tucker, 1954	Rosaura 49	28° 25′ N., 13° 34′ W.	1.ii.1938	1,300	—	—	1
					Species total (for Atlantic)		>69

ATLANTIC OCEAN

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
2. *Halosaurus johnsonianus* Vaillant, 1888							
Vaillant, 1888	Talisman XIII	35° 07′ N., 7° 18′ W.	11.vi.1883	1,216	m. & cor.	10° C.	1
	XXXII	32° 34′ N., 9° 49′ W.	16.vi.1883	1,590	th. m.	—	1
	XXXIII	32° 31′ N., 9° 49′ W.	17.vi.1883	1,350	r. m.	—	10
	XXXIII[2]	32° 31′ N., 9° 48′ W.	17.vi.1883	834	m.	11° C.	1
	XLI	30° 01′ N., 11° 46′ W.	24.vi.1883	2,115	gy. m. bkn. shs.	—	6
	XLII	29° 58′ N., 11° 41′ W.	25.vi.1883	2,104	m. & bkn. shs.	—	3
	XLV	29° 08′ N., 12° 26′ W.	26.vi.1883	1,235	sft. ye. m.	8.5° C.	1
	XLIX	28° 37′ N., 13° 02′ W.	27.vi.1883	865	ye. m.	7·0° C.	1
	L	28° 35′ N., 13° 10′ W.	27.vi.1883	975	ye. m.	7·2° C.	1
	LXXII	25° 39′ N., 16° 02′ W.	9.vii.1883	882	my. s. cor. shs.	—	18
	LXXIX	23° 53′ N., 17° 16′ W.	11.vii.1883	1,232	gy. m.	5·8° C.	33
	LXXXI	23° 50′ N., 17° 17′ W.	11.vii.1883	1,139	gy. m.	6·2° C.	7
	XCIII	20° 44′ N., 18° 07′ W.	14.vii.1883	1,495	gn.-sh. my. s.	4·5° C.	13
Collett, 1896	Hirondelle 112	38° 34′ N., 28° 06′ W.	1.vii.1887	1,287	fn. s.	—	1
	233	38° 33′ N., 28° 08′ W.	18.viii.1888	1,300	m. & s.	9·8° C.	1
Roule, 1919	Pr. Alice 553	37° 42′ N., 25° 05′ W.	3.vii.1895	1,385	my. s.	—	3
Koefoed, 1927	M. Sars 23	35° 32′ N., 07° 07′ W.	6.v.1910	1,215	ye. m.	<10·2° C.	16
Tucker, 1954	Rosaura 49	28° 25′ N., 13° 34′ W.	1.ii.1938	1,300	—	—	1
Pérès, 1958	F.N.R.S. III bathyscaphe	38° 17′ N., 09° 13′ W.	23.viii.1956	1,690	r. m.	*c.* 4° C.	" many "
					Species total (for Atlantic)		>118
3. *Halosaurus guentheri* Goode & Bean, 1895							
Goode & Bean, 1895	Albatross 2722	39° 13′ N., 72° 01′ W.	20.ix.1886	1,086	gn. m.	—	1
Springer & Bullis, 1956	Oregon 349	29° 09′ N., 87° 38′ W.	22.v.1951	914	blu. m.	—	—
	640	29° 01′ N., 88° 24′ W.	19.ix.1952	869	—	—	—
					Species total (for Atlantic)		>3
					Total number of the genus *Halosaurus* (for Atlantic)		>190

4. *Aldrovandia macrochir* (Guenther, 1878)

Guenther, 1878	Challenger V	35° 47′ N., 8° 23′ W.	28.i.1873	1,993	glob. oz.	3·5° C.	1
Vaillant, 1888	Talisman XXXIX	30° 08′ N., 11° 42′ W.	23.vi.1883	2,200	th. m.	*(4·0° C.)	9
	CXXX	37° 55′ N., 27° 02′ W.	16.viii.1883	2,235	sft. gy. m.	*(*c*.4·0° C.)	1
	CXXXI	38° 38′ N., 25° 06′ W.	22.viii.1883	2,995	sft. wh. m.	3·4° C.	1
Gill, 1881	Blake Ag. 308	41° 24′ N., 65° 35′ W.	29.vi.1880	2,271	dk. gy. m.	3·2° C.	—
(" H. goodei ")	Ag. 325	33° 35′ N., 76° 00′ W.	14.vii.1880	1,183	glob. oz.	3·8° C.	—
Goode & Bean, 1895	Albatros 2035	— — N., — — W.	17.vii.1883	2,491	glob. oz.	*(3·2° C.)	3
	2037	38° 53′ N., 69° 23′ W.	18.vii.1883	3,166	glob. oz.	3·2° C.	1
	2051	39° 41′ N., 69° 20′ W.	1.viii.1883	2,023	bl. m. & oz.	3·8° C.	>11
	2052	— — N., — — W.	1.viii.1883	2,008	glob. oz.	7·2° C.	>10
	2074	41° 43′ N., 65° 21′ W.	3.ix.1883	2,257	m. & sts.	4·4° C.	—
	2077	41° 09′ N., 66° 02′ W.	4.ix.1883	2,295	blu. m.	3·8° C.	—
	2106	37° 41′ N., 73° 03′ W.	6.xi.1883	2,738	glob. oz.	5·7° C.	—
	2111	35° 09′ N., 74° 57′ W.	9.xi.1883	1,715	gn. m.	—	—
	2116	35° 45′ N., 74° 31′ W.	11.xi.1883	1,624	bl. m. & fn. s.	3·8° C.	—
	†2140	17° 36′ N., 76° 46′ W.	11.iii.1884	1,767	s.	4·3° C.	—
(Tanner, 1886 p. 46)		38° 27′ N., 73° 02′ W.	12.ix.1884	2,136	—	—	" a few "
	2533	40° 16′ N., 67° 26′ W.	15.vii.1885	1,514	br. oz.	3·7° C.	—
	2550	39° 44′ N., 70° 30′ W.	9.viii.1885	1,977	br. m.	3·5° C.	—
	2562	39° 15′ N., 71° 25′ W.	11.viii.1885	2,623	gy. oz.	2·9° C.	—
	2563	39° 18′ N., 71° 23′ W.	11.viii.1885	2,601	by. oz.	3·0° C.	—
	2564	39° 22′ N., 71° 23′ W.	11.viii.1885	2,452	gy. oz.	2·9° C.	—
	2571	40° 09′ N., 67° 09′ W.	1.ix.1885	2,480	gy. glob. oz.	3·2° C.	—
Collett, 1896	Hirondelle 209	39° 18′ N., 31° 02′ W.	31.vii/1.viii. 1888	1,372	my. s. w. bkn. shs.	—	2
Roule, 1919	Pr. Alice 575	38° 27′ N., 26° 30′ W.	13.vii.1895	1,165	my. s.	6·8° C.	1
	698	39° 11′ N., 30° 44′ W.	18.vii.1896	1,846	gy. sy. m.	*>5·5° C.	1
	738	37° 40′ N., 26° 26′ W.	7.viii.1896	1,919	sy. m.	4·0° C.	1
	Pr. Alice II 1331	38° 40′ N., 26° 00′ W.	9.viii.1902	1,805	my. s.	*>3·8° C.	4
	1334	39° 30′ N., 29° 02′ W.	13.viii.1902	1,900	glob. oz.	4·1° C.	2
Zugmayer, 1911	Pr. Alice II 2990	43° 45′ N., 9° 41′ W.	18.viii.1910	2,320	glob. oz.	3·7° C.	2
Roule & Angel, 1933	Hirondelle II 3150	38° 01′ N., 25° 21′ W.	27.viii.1911	1,740	—	—	1
Gilchrist 1906,	P. Fauré Shrimp Trawl No.						
	16,893	34° 44′ S., 17° 45′ E.	Sept. 1903	1,646	gn. m. & rks.	—	1
	16,937	34° 44′ S., 17° 45′ E.	Sept. 1903	1,646	gn. m. & rks.	—	1
	17,257	34° 30′ S., 17° 39′ E.	Sept. 1903	1,701	gn. m. & rks.	—	1
	17,293	34° 29′ S., 17° 41′ E.	Sept. 1903	1,628	gn. m. & rks.	—	1
Gilchrist & von Bonde, 1924	Pickle 526	33° 17′ S., 16° 24′ E.	17.xi.1921	2,560	—	—	2

† And a large earthenware jar (Tanner, 1886 : 20).

* At neighbouring Stations.

ATLANTIC OCEAN

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
Koefoed, 1927	M. Sars 25	35° 46′ N., 8° 16′ W.	8.v.1910	2,055	ye. m. (glob. oz.)	<5·27° C.	5
	35	27° 27′ N., 14° 52′ W.	18.v.1910	2,603	ye. glob. oz.	—	2
	53	34° 59′ N., 33° 01′ W.	8.vi.1910	2,615	wh. glob. oz.	<4·4° C.	7
	88	45° 26′ N., 25° 45′ W.	18.vii.1910	3,120	wh. glob. oz.	—	1
	95	50° 22′ N., 11° 44′ W.	26–27.vii. 1910	1,797	gy. glob. oz.	—	3
					Species total (for Atlantic)		>92
5. *Aldrovandia phalacra* (Vaillant, 1888)							
Vaillant, 1888	Talisman XVI	34° 01′ N., 8° 32′ W.	13.vi.1883	2,190	m.	4·5° C.	1
	XXII	33° 47′ N., 9° 03′ W.	14.vi.1883	1,635	m.	6·5° C.	2
	XXXI	32° 37′ N., 9° 47′ W.	16.vi.1883	1,103	m.	*(3·5° C.)	2
	XLII	29° 58′ N., 11° 41′ W.	25.vi.1883	2,104	gy. m. & bkn. shs.	*(5·0° C.)	1
	LXXIII	25° 39′ N., 17° 15′ W.	9.vii.1883	1,435	gy. m.	—	1
	LXXIX[2]	23° 53′ N., 17° 17′ W.	11.vii.1883	1,250	gy. m.	6·0° C.	3
	CXXI	37° 35′ N., 29° 26′ W.	12.viii.1883	1,442	gy. m.	7·0° C.	1
	CXXIX	38° 00′ N., 27° 03′ W.	16.viii.1883	2,220	sft. gy. m.	*(4·0° C.)	1
Roule, 1919	Pr. Alice 703	39° 21′ N., 31° 05′ W.	19.vii.1896	1,360	—	—	1
	Pr. Alice II 1123	27° 41′ N., 17° 53′ W.	15.vii.1901	1,786	hd. bm.	5·2° C.	3
	1209	16° 34′ N., 23° 03′ W.	18.viii.1901	1,477	—	4·7° C.	1
Zugmayer, 1911	Pr. Alice II 2989	43° 45′ N., 9° 41′ W.	18.viii.1910	2,320	glob. oz.	3·7° C.	1
					Species total (for Atlantic)		18

6. *Aldrovandia affinis* (Guenther, 1877)

Goode & Bean, 1895	Blake Ag. 29	24° 36′ N., 84° 05′ W.	(Jan?) 1878	1,746	—	4·1° C.	—
	Albatross 2072	41° 53′ N., 65° 35′ W.	2.ix.1883	1,569	gy. m.	3·8° C.	–
	2181	39° 29′ N., 71° 46′ W.	23.vii.1884	1,267	gy. m., fn. s.	3·8° C.	—
	2216	39° 47′ N., 70° 30′ W.	22.viii.1884	1,761	gn. m.	4·1° C.	—
	2231	38° 29′ N., 73° 09′ W.	12.ix.1884	1,765	gy. oz.	2·6° C.	—
	2380	28° 02′ N., 87° 43′ W.	2.iii.1885	2,615	br. m.	4·4° C.	—
	2381	28° 05′ N., 87° 56′ W.	2.iii.1885	2,432	lt. br. m.	—	—
	2533	40° 16′ N., 67° 26′ W.	15.vii.1885	1,514	br. oz.	3·6° C.	—
	2729	36° 26′ N., 74° 32′ W.	25.x.1886	1,242	dk. gn. m.	—	—
Gilchrist, 1906	P. Fauré						
	Ref. no. 17714	34° 28′ S., 17° 43′ E.	?9.ix.1903	1,152	reg. of	—	2
	Ref. no. 17742	34° 28′ S., 17° 46′ E.	?9.ix.1903	914	gn. m. & rks.	—	1
Gilchrist & von Bonde	Pickle 77	33° 48′ S., 17° 07′ E.	11.v.1920	1,381	—	—	1
	251	33° 43′ S., 17° 24′ E.	23.xi.1920	1,116	—	—	1
	522	33° 24′ S., 16° 38′ E.	15.xi.1921	2,195	—	—	8
	526	33° 17′ S., 16° 24′ E.	17.xi.1921	2,560	—	—	3
	534	33° 30′ S., 16° 45′ E.	29.xi.1921	1,847	—	—	2
	542	33° 41′ S., 17° 09′ E.	8.xii.1921	1,061	—	—	1
Grey, 1955 (Springer & Bullis, 1956)	Oregon 1303	28° 47′ N., 87° 50′ W.	26.v.1955	2,195	gy. m.	—	20
					Species total (for Atlantic)		>48

6a. *Specimens of uncertain identity* ; probably *A. affinis*

Gilchrist, 1906 (p. 171)	P. Fauré	34° 57′ S., 17° 51′ E.		1,390		—	1
Parr, 1937	Pawnee 54	21° 16′ N., 71° 18′ W.	12.iv.1927	*c.* 1,321? (1,981 m. of wire out)	—	—	4
Harrisson, 1966	Discovery 4745	29° 50′ N., 22° 57′ W.	23.ix.1961	1,100 (bottom at *c.* 5,200 m.)	Midwater trawl	—	1 leptocephalus
					Species total (for Atlantic)		6

ATLANTIC OCEAN

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
7. *Aldrovandia rostrata* (Guenther, 1878)							
Guenther, 1878	Challenger 63	35° 29′ N., 50° 53′ W.	19.vi.1873	5,029	glob. oz.	—	1
Roule, 1919	Pr. Alice II 1193	15° 17′ N., 23° 01′ W.	15.viii.1901	1,311	gn. my. s.	5·8° C.	1
					Species total (for Atlantic)		2
8. *Aldrovandia gracilis* Goode & Bean, 1895							
Goode & Bean, 1895	Blake 163 Ag.	16° 03′ N., 61° 52′ W.	20.i.1879	1,406	oz. & s.	4·3° C.	1
	Albatross 2380	28° 02′ N., 87° 43′ W.	2.iii.1885	2,615	br. m.	4·4° C.	1
	2381	28° 05′ N., 87° 56′ W.	2.iii.1885	2,432	lt. br. m.	—	1
Roule & Angel, 1933	Hirondelle II 3476	42° 31′ N., 63° 40′ W.	6.ix.1913	1,380	—	—	1
Grey, 1955	Oregon 1303	28° 47′ N., 87° 50′ W.	26.v.1955	2,195	gy. m.	—	21
					Species total (for Atlantic)		25
			Total number of the genus *Aldrovandia* (for Atlantic)				>191

INDIAN OCEAN

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
1. *Halosaurus carinicauda* (Alcock, 1889)							
Alcock, 1889	Investigator 10	*c.* 11° 23′ N., 92° 42′ E.	12.iv.1888	896	—	—	1
Weber, 1913	Siboga 18	7° 28′ S., 115° 24′ E.	18.iii.1899	1,018	fn. m.	—	1
					Species total (for Indian Ocean)		2

2. *H. parvipennis* Alcock, 1892							
Alcock, 1892	Investigator 122	12° 05′ N., 71° 33′ E.	21.x.1891	1,609	glob. oz.	4·4° C.	1
1899	177	13° 47′ N., 73° 07′ E.	5.v.1894	1,163	gn. m.	6·7° C.	1
	217	6° 56′ N., 72° 53′ E.	21.x.1896	839	s.	—	1
Norman, 1939	Mabahiss 33	13° 41′ N., 48° 17′ E.	15.x.1933	1,295	gn. m.	—	1
	143	5° 16′ S., 73° 23′ E.	30.iii.1934	797	gn. s.	<7·9° C.	1
2a. Probably *H. parvipennis*							
Marshall & Bourne, 1965	Atlantis 1	12° 51′ N., 45° 57′ E.	vi.1958	1,240	—	—	<4
					Species total (for Indian Ocean)		<9
3. *H. pectoralis* McCulloch, 1926							
McCulloch, 1926	Endeavour	Gt. Australian Bight S. of Eucla	13.v.1913	823	—	—	3
					Species total (for Indian Ocean)		3
			Total number of the genus *Halosaurus* (for Indian Ocean)				14
4. *Aldrovandia macrochir* (Guenther, 1878)							
Guenther, 1878	Challenger 146	46° 46′ S., 45° 31′ E.	29.xii.1873	2,515	glob. oz.	2·0° C.	4
					Species total (for Indian Ocean)		4
5. *A. affinis* (Guenther, 1877)							
Alcock, 1889	Investigator 2	6° 32′ N., 79° 37′ E.	5.v.1886	1,234	gn. m. & bar. nods.	—	2
1890	104	11° 12′ N., 74° 25′ E.	3.v.1890	1,829	ol. gn. m.	3·6° C.	4
1896	217	6° 56′ N., 72° 53′ E.	21.x.1896	839	s.	—	1†
Weber, 1913	Siboga 286	8° 50′ S., 127° 02′ E.	19.i.1900	883	m.	—	1
	300	10° 48′ S., 123° 23′ E.	30.i.1900	918	m.	—	1
Norman, 1939	Mabahiss 118	4° 06′ S., 41° 10′ E.	17.i.1934	1,789	glob. oz.	—	1
	158	4° 42′ N., 72° 42′ E.	7.iv.1934	1,117	—	—	1
Mead, 1965	Anton Bruun 349 B	26° 44′ S., 65° 05′ E.	26.vi.1964 bottom at:	1,470 4,571	Isaacs-Kidd midwater trawl	—	1†
					Species total (for Indian Ocean)		12

† "*H. nigerrimus*" see note on p. 462.

INDIAN OCEAN

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
6. *A. mediorostris* (Guenther, 1887)							
Alcock, 1894	Investigator 150	7° 05′ N., 75° 04′ E.	29.xi.1893	1,315	fn. cor. s.	—	1
Weber, 1913	Siboga 18	7° 28′ S., 115° 24′ E.	18.iii.1899	1,018	fn. m.	—	1
					Species total (for Indian Ocean)		2
7. *A. phalacra* (Vaillant, 1888)							
Brauer, 1908	Valdivia 257	1° 48′ N., 45° 42′ E.	27.iii.1899	1,644	fm. gy. br. glob. oz.	—	1
					Species total (for Indian Ocean)		1
			Total number of the genus *Aldrovandia* (for Indian Ocean)				19

PACIFIC OCEAN

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
1. *H. radiatus* Garman, 1899							
Garman, 1899	Albatross 3354	7° 09′ N., 80° 50′ W.	23.ii.1891	589	gn. m.	3·8° C.	—
	3394	7° 21′ N., 79° 35′ W.	10.iii.1891	934	dk. gn. m.	5·4° C.	—
	3396	7° 32′ N., 78° 36′ W.	11.iii.1891	474	gy. m. & s.	8·5° C.	—
Bussing, 1965	Eltanin 34	7° 48′ S., 81° 23′ W.	6.vii.1962	680	midwater trawl (bottom at 5,050 m.)	—	1
					Species total (for Pacific)		>4

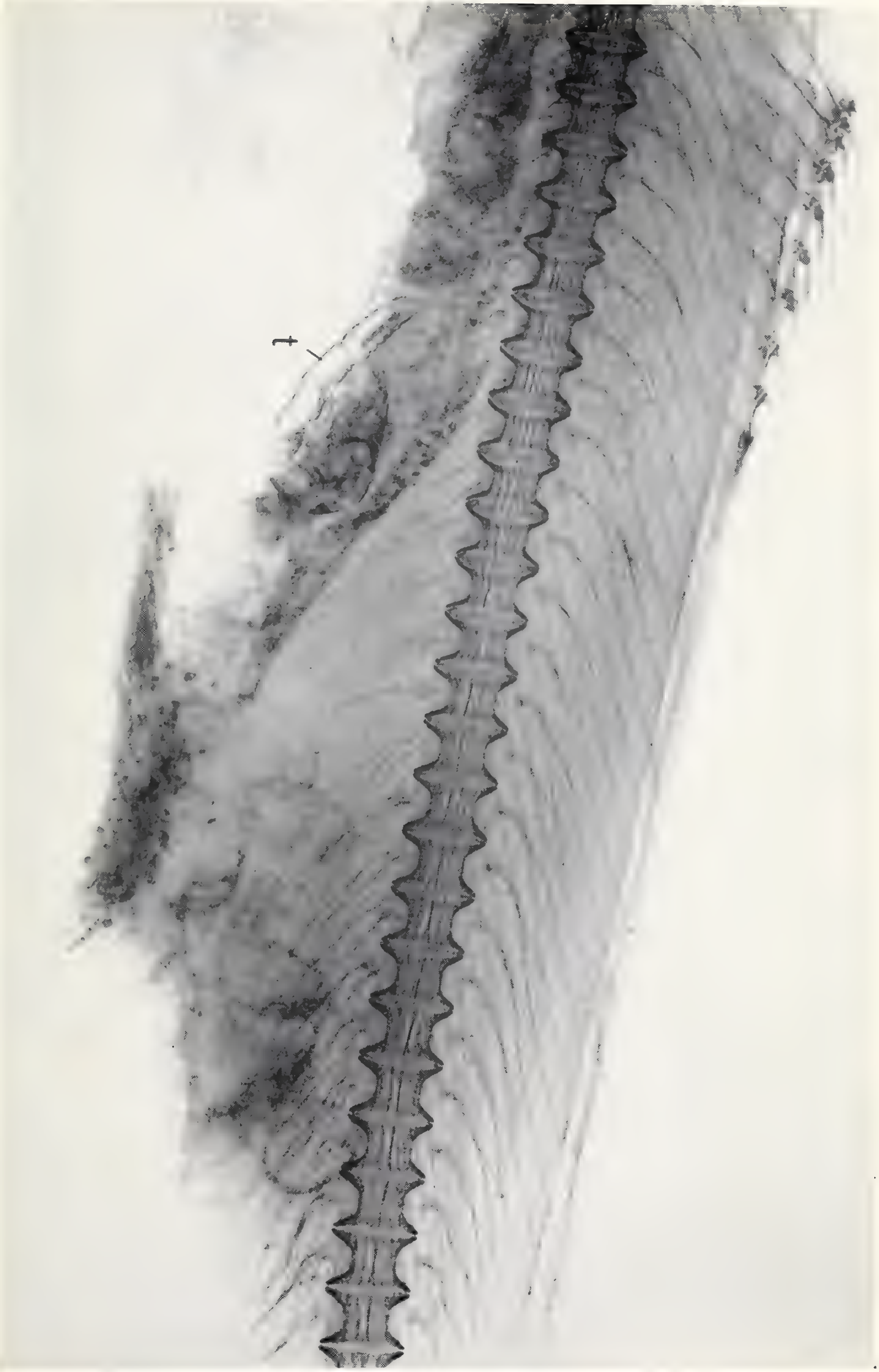
2. *Halosaurus attenuatus* Garman, 1899							
Garman, 1899	Albatross 3413	2° 34′ N., 92° 06′ W.	5.iv.1891	2,487	glob. oz.	2·2° C.	1
Townsend & Nichols, 1925	Albatross 5676	25° 31′ N., 113° 29′ W.	17.iii.1911	1,180	gn. m. fn. s. glob.	3·8° C.	1
					Species total (for Pacific)		2
3. *H. ridgwayi* (Fowler, 1933)							
Fowler, 1933	Albatross D. 5527	9° 23′ N., 123° 43′ E.	11.viii.1909	717	glob. oz.	11·8° C.	7
					Species total (for Pacific)		7
			Total number of the genus *Halosaurus* (for Pacific)				>13
4. *Aldrovandia affinis* (Guenther, 1877)							
Guenther, 1877	Challenger 235	34° 07′ N., 138° 0′ E.	4.vi.1875	1,033	gn. m.	3·3° C.	2
					Species total (for Pacific)		2
5. *A. mediorostris* (Guenther, 1887)							
Guenther, 1887	Challenger 207	12° 21′ N., 122° 15′ E.	16.i.1875	1,280	blu. m.	10·9° C.	1
					Species total (for Pacific)		1
6. *A. verticalis* (Gilbert, 1905)							
Gilbert, 1905	Albatross 3985	22° 04′ N., 159° 15′ W.	10.vi.1902	872	gy. s. w. shr. deb.	4·4° C.	—
	4141	22° 04′ N., 159° 16′ W.	2.viii.1902	1,156	vol. s. w. foram.	4·9° C.	—
	4151	23° 16′ N., 161° 46′ W.	5.viii.1902	1,593	cor. s.	3·2° C.	—
					Species total (for Pacific)		>3
7. *A. proboscoidea* (Gilbert, 1905)							
Gilbert, 1905	Albatross 4111	21° 25′ N., 157° 25′ W.	24.vii.1902	859	fn. s., rks.	4·4° C.	—
					Species total (for Pacific)		>1

PACIFIC OCEAN

First mention of record	Ship and Station No.	Position (Long. fm. Greenwich)	Date of capture	Depth (m.)	Bottom deposit	Bottom Temp.	Number of Halosaurs taken
8. *A. kauiensis* (Gilbert, 1905)							
	Albatross 3887	21° 17′ N., 156° 41′ W.	17.iv.1902	1,479	fn. ye. s. & glob. oz.	4·1° C.	—
	3977	23° 07′ N., 162° 12′ W.	2.vi.1902	1,602	cor. s. for r.	3·3° C.	—
	3989	22° 07′ N., 159° 15′ W.	11.vi.1902	914	cor. s. for r.	3·0° C.	—
	4018	22° 03′ N., 159° 14′ W.	21.vi.1902	1,470	foram. shs. & mang.	2·8° C.	—
	4019	22° 16′ N., 159° 14′ W.	21.vi.1902	1,006	gy. s. for r	3·2° C.	—
					Species total (for Pacific)		>5
					Total number of the genus *Aldrovandia* (for Pacific)		>12

PLATE 1

X-radiograph of type of *Aldrovandia rostrata,* showing intermuscular bones and the clear image of a tanaid (=*t*), in the hind-gut.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